ECOLOGY

VOL. 32 OCTOBER, 1951 No. 4

SOME QUANTITATIVE ASPECTS OF ALGAL GROWTH IN LAKE MENDOTA[1]

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INTRODUCTION

The seasonal fluctuations in the quantities and kinds of phytoplankton in lakes has received the attention of limnologists for many years. For southern Wisconsin lakes, a good general description of the annual phytoplankton cycles of pelagic waters has been presented by Birge and Juday (1922). Causes of these fluctuations have sometimes been explained on the basis of the levels of chemical nutrients, especially phosphorus and nitrogen compounds, which are present in natural waters, though few generalizations of real or supposed biological and chemical relationships have thus far had wide application.

At the present only a limited amount of information has been gained from experimental algal cultures which can be applied directly toward an understanding of the usually different conditions existing in various natural waters. The experiments of Chu (1942), Rodhe (1948), and Gerloff, Fitzgerald, and Skoog (1950) have, however, been pioneering efforts in this direction. The broader concept of ecological succession of algal species in relation to the nutrients consumed and liberated, which has been discussed extensively by Pearsall (1932), Hutchinson (1944), and Rodhe (1948), among others, has revealed that certain generalizations accounting for algal periodicities are possible, though Hutchinson has emphasized the complexity of these successional phenomena and the necessity of limiting discussions to the simplest situations in individual lakes.

On the basis of present ecological and chemical information, it has been difficult or impossible to account for the sudden and sporadic outbursts of various phytoplankton species, especially the Myxophyceae which often comprise the "nuisance" blooms of eutrophic lakes (Hasler 1947).

The overall seasonal cycles of some of the phytoplankters for the pelagic areas of Lake Mendota have been described by Birge and Juday (1922), but the more diverse quantitative relationships of the phytoplankton at the inlets of rivers and over littoral areas have not been examined heretofore in relation to the possible contributions from these environments to the lake as a whole. Accordingly, the purpose of this preliminary investigation was to ascertain whether phytoplankton fluctuations, especially of the blue-green algae, could have local origins within a lake and what, if any, were the influences of the

[1] Supported in part from funds received from the Wisconsin Alumni Research Foundation. Grateful acknowledgment is made for generous aid by the following: Erwin R. Beilfuss, Park College, Mo., for faithful processing of samples; James H. Torrie, Kenneth S. Arnold, and John C. Neess in statistics; Richard I. Evans in alga identification; G. A. Rohlich and W. L. Lea in the interpretation of chemical data; L. A. Joos in the interpretation of weather data; and W. B. Sarles for arranging facilities and coordinating the program with the above co-workers.

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underlying sediments, plants beds, weather conditions, and water movements.

Data dealing with the chemical composition of the water at the times alga collections were made for this study have been described by Emelity and Hanson (1949).

Distribution of Algae in Pelagic Areas

Procedure

A study was made of the yearly distribution of phytoplankton in waters over three major depressions of Lake Mendota. Collections were obtained from just below the surface and at a depth of 10 m. at localities designated PB 3, U 3, and M in Figure 1. These collections were designed to yield information on the depth, areal, and temporal distributions of the pelagic phytoplankton content of the lake throughout the year.

In order to evaluate the quantity of phytoplankton present, a modification of the method described by Gessner (1944) was used to determine the total chlorophyll content of the water samples. Immediately after collection, three-liter samples of water were filtered through a Whatman No. 42 paper with the aid of slight suction. Two-liter samples were occasionally used when the water was very turbid. The filter paper was then washed with several milliliters of boiling water, not to destroy the chlorophyllase as Gessner has suggested, but to aid in breaking up algal cell walls, thus facilitating pigment extraction. After air-drying, the filter paper was placed in a Petri dish and 12 ml. of absolute methyl alcohol was added. The dish was covered and allowed to stand in the dark. After 24 hours the contents of the dish were filtered into a 25 ml. volumetric flask and made up to volume by absolute methyl alcohol washings of the filter paper and

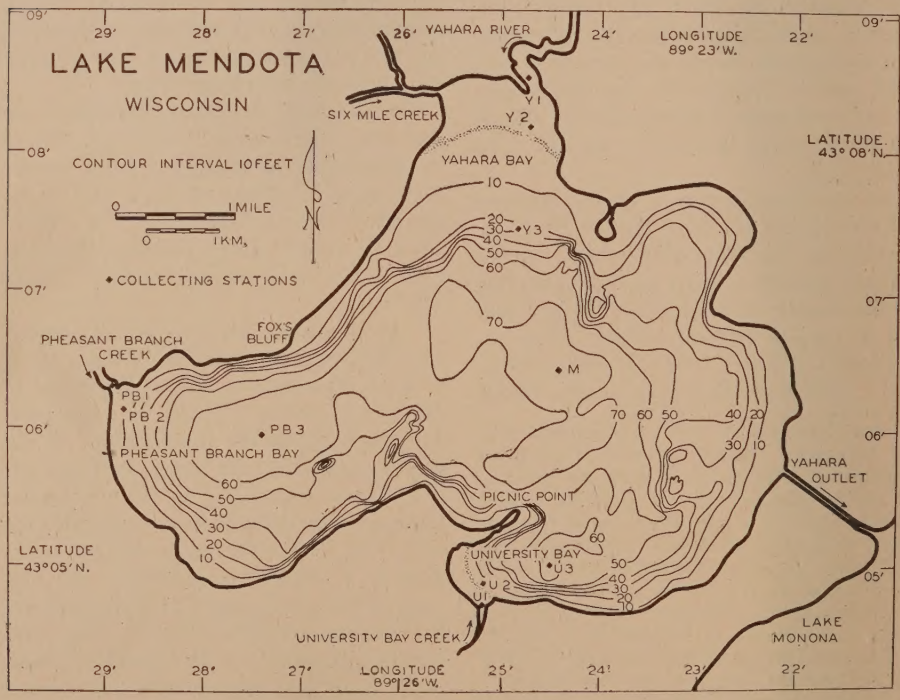

Fig. 1. Map of Lake Mendota, Wisconsin.

TABLE I. *Averages of chlorophyll contents in milligrams per cubic meter of surface and 10-meter levels over three depressions in Lake Mendota. Analysis of variance data are given*

Season	Date	University Bay U 3	Pheasant Branch Bay PB 3	Central Lake M	Means
Summer stagnation	21 VII 48	5.0	4.2	3.5	4.25
	23 VIII 48	6.0	4.5	3.2	4.58
	27 IX 48	29.0	19.2	37.5	28.58
Means		13.33	9.33	14.75	12.47
Autumn circulation	18 X 48	27.2	31.8	28.8	29.25
	8 XI 48	11.8	10.8	12.0	11.50
	30 XI 48	3.8	3.2	4.2	3.75
Means		14.25	15.25	15.00	14.83
Winter stagnation	4 I 49	5.8	7.5	5.8	6.33
	9 II 49	2.5	2.0	1.8	2.08
	1 III 49	7.2	6.2	4.5	6.00
Means		5.17	5.25	4.00	4.81
Spring circulation	4 IV 49	50.0	42.8	34.2	42.33
	4 V 49	3.5	2.8	2.2	2.83
	23 V 49	7.0	7.0	7.8	7.25
Means		20.17	17.50	14.75	17.47
Yearly means		13.23	11.83	12.13	12.40

Analysis of variance

Source of variation	df	Mean square	*F*
Dates	11	1062.09	64.447[a]
Seasons	3	535.98	32.523[a]
Dates within seasons	8	1259.38	76.419[a]
Depressions PB 3, U 3, and M	2	13.01	—
Depths	1	9.03	—
Double and triple interactions not involving "dates within seasons"	17	(none is significant)	
Error (all triple and quadruple interaction terms having "dates within seasons")	40	16.48	

[a] Significant at 1% level or less.

contents. The pigment extract was then placed in an Evelyn colorimeter standardized with a methyl alcohol blank; percentage light transmission was measured when a No. 660 filter was inserted. By use of light transmission curves drawn up for known concentrations of chlorophyll-a and chlorophyll-b in the ratio of 3 : 1, the concentrations of the chlorophyll in mg./l. or mg./cu.m. were obtained. These standard curves had been prepared under the direction of J. F. Stauffer, Department of Botany, University of Wisconsin.

Analysis of results

The chlorophyll contents of the pelagic collections from July, 1948, through May, 1949, expressed as averages of collections at the surface and at a depth of 10 m., are given in Table I. These data are divided into four seasons on the basis of summer hypolimnetic stagnation, autumn circulation, winter stagnation, and spring circulation periods whose durations were determined from vertical series of temperature readings taken throughout the year. It is obvious from a perusal of the

group means in Table I that the depression variability is neither great nor consistent in any one direction. However, from one collection date to the next, there is considerable variation with respect to both the yearly and seasonal means. Further, the seasonal means vary widely about the yearly mean. The analysis of these data is given in the same table with appropriate F-tests. (See Snedecor, 1946, for F-tables.) The tests of significance indicate that the greatest variations in the chlorophyll contents accompanied temporal differences, while the chlorophyll differences from depression to depression and from surface to 10 m. were not significant.

Horizontal Distribution of Algae in Surface Waters

It is known that large amounts of potential nutrient materials for algal growth are washed into Lake Mendota from inflowing streams (Emelity and Hanson 1949). Just what effect this nutrient influx may have on the quantity at the river mouths and in the weedy littoral beyond the river mouths as compared to the more or less uniform pelagic areas was the object of this phase of the present study.

Procedure

Yahara, Pheasant Branch, and University Bay areas were studied. Collection stations (Fig. 1) were established at the Yahara River inlet, at the inlet of Pheasant Branch Creek, and at the mouth of the small creek entering University Bay, respectively designated Y 1, PB 1, and U 1; slightly beyond each of these three inlets are dense weed beds where stations are indicated as Y 2, PB 2, and U 2; and farther out in the lake beyond the littoral zone were pelagic stations Y 3, PB 3, and U 3. From July, 1948, through May, 1949, water samples were taken from 0.5 m. at these stations and chlorophyll contents determined.

Analysis of results

Results are given in Table II. In making an analysis of these data, it appeared that the very high chlorophyll contents for some stations, e.g., at the Yahara River mouth, would have an unduly great influence in the analysis of variance. To circumvent such difficulties, logarithmic

Table II. *Chlorophyll contents in milligrams per cubic meter of surface waters from selected locations in Lake Mendota*

Season	Date	University Bay			Pheasant Branch Bay			Yahara Bay		
		River mouth	Weedy littoral	Pelagic	River mouth	Weedy littoral	Pelagic	River mouth	Weedy littoral	Pelagic
		U 1	U 2	U 3	PB 1	PB 2	PB 3	Y 1	Y 2	Y 3
Summer stagnation	16 VII 48	11.5	30.0	40.5	10.0	86.5	13.0	127.0	12.5	20.0
	30 VII 48	14.5	10.5	20.0	9.0	10.5	25.5	56.5	9.0	7.5
	18 VIII 48	14.0	11.5	9.5	8.5	10.0	9.5	56.5	40.5	8.0
	8 IX 48	51.5	18.0	23.0	41.5	26.5	20.0	49.0	18.5	22.5
Autumn circulation	4 X 48	14.5	—	24.5	27.0	28.5	22.0	46.5	19.5	24.0
	25 X 48	20.0	18.0	21.5	21.0	23.0	39.0	75.5	60.0	26.0
	15 XI 48	6.5	4.0	5.0	7.5	36.5	3.5	80.5	33.0	10.0
	7 XII 48	5.5	5.0	24.5	8.0	24.0	5.5	23.0	16.0	6.5
Winter stagnation	11 I 49	5.0	5.0	40.0	8.0	18.5	6.5	4.0	14.0	3.0
	18 II 49	—	4.0	2.5	6.5	6.0	3.0	3.5	5.0	2.5
Spring circulation	11 IV 49	13.0	29.5	42.5	27.5	38.0	49.5	199.0	35.5	27.5
	21 IV 49	11.5	22.5	21.0	14.5	28.0	24.0	194.5	51.0	27.5
	11 V 49	4.5	3.0	3.0	9.5	1.5	2.0	52.0	19.5	9.0
	21 V 49	12.0	10.5	10.5	9.5	10.5	9.0	12.5	7.5	8.0

TABLE III. *Analyses of logarithms of chlorophyll content data given in Table II for Lake Mendota surface waters for three seasons*

Source of variation	Summer period		Autumn period		Spring period	
	df	Mean square	df	Mean square	df	Mean square
Dates (D)	3	0.221952[a]	3	0.434766[a]	3	1.292960[a]
Bays (B)	2	0.088702	2	0.473077[a]	2	0.608578
Stations (S)	2	0.128680	2	0.075275	2	0.129492
(D x B)	6	0.034766	6	0.058843	6	0.143745[a]
(D x S)	6	0.056190	6	0.057029	6	0.051758
(B x S)	4	0.260317[a]	4	0.242241[a]	4	0.188093[a]
(D x B x S)	12	0.078397	11[b]	0.044833	12	0.039853

[a] Possibly significant at the 5% level (see text).
[b] One df lost due to calculation of missing value.

transformations were made (Bartlett 1947).

The analyses for three seasons only are considered; the winter stagnation season, whose two series of collections are inadequate for analysis, is omitted. Since the seasonal variability has been demonstrated (Table I), these analyses are carried out on an individual seasonal basis as shown in Table III. Though no replicate collections were made, the mean squares of single factors may be compared to the mean squares of the respective two-factor interactions. Correspondingly the two-factor interactions may be compared to the three-factor interaction. There is no error mean square as such.[3] The statistical significance of results obtained by this method are to be considered as suggestive or tentative rather than conclusive.

The three bays were essentially similar quantitatively during the summer and spring periods. During autumn, however, University Bay chlorophyll contents were low enough and Yahara Bay values were high enough to suggest statistically significant differences. For each of the three seasons analyzed, Yahara Bay had the greatest quantity of phytoplankton. The high values of the Yahara River mouth data need not be considered greatly distorted when compared to the values for the remainder of the lake since the drainage into the Yahara Bay is the largest and richest in nutrient materials as compared to the drainage supplied to Pheasant Branch and University Bays.

From river mouths to weed beds to pelagic areas, the bays were individually dissimilar. This condition is reflected in the station x bay interactions which seem to exist throughout the year, apparently caused by the high values at the Yahara River mouth and at the weedy littoral of Pheasant Branch Bay and to the low values at the Yahara pelagic and the University Bay weedy littoral stations. Samples of substrata from the latter two stations had sandy consistency in contrast to the finely divided muds of the other stations.

The date x bay interaction during the spring period means that the relative magnitudes of the chlorophyll contents for

[3] The procedures and justifications for such calculations are summarized by Fisher (1947). The calculations of significant F-values may be shown by using letter designations for the appropriate mean squares and degrees of freedom shown in Table III. Using one asterisk to denote possible significance at the 5% level, and two for the 1% level, the following analyses may be shown:

Summer period:
Dates, $F = D/(D \times B) = 6.384^*$.
Bays x Stations, $F = (B \times S)/(D \times B \times S) = 3.320^*$.

Autumn period:
Dates, $F = D/(D \times B) = 7.389^*$, and $F = D/(D \times S) = 7.624^*$.
Bays, $F = B/(D \times B) = 8.040^*$.
Bays x Stations, $F = (B \times S)/(D \times B \times S) = 5.403^*$.

Spring period:
Dates, $F = D/(D \times B) = 8.995^*$, and $F = D/(D \times S) = 24.981^{**}$.
Dates x Bays, $F = (D \times B)/(D \times B \times S) 3.607^*$.
Bays x Stations, $F = (B \times S)/(D \times B \times S) = 4.720^*$.

the three bays changed from date to date. Whereas the chlorophyll content at Pheasant Branch showed some tendency to remain intermediate, that of University Bay tended to decrease relatively, while that of Yahara Bay tended to increase as the spring season progressed.

The Potentialities of Lake Sediments in Initiating and Supporting Algal Growth

The work of Lind (1940) and Mortimer (1941–1942) has emphasized the diversities and potentialities of sediments in influencing algal growth from both quantitative and qualitative aspects. With the knowledge that different areas of Lake Mendota support greatly differing quantities of algae, an inquiry into the possible effects of the underlying sediments was instituted.

Cultures of muds taken during the winter

Procedure. From the same three stations in each of the three bays discussed in the preceding section, samples of mud were obtained beneath the ice on 11 March 1949. For each station six 100 g. samples of the sediment were weighed out and strained and washed through bolting cloth (17.4 meshes per cm) using 250 ml. of distilled water. The straining operation served to eliminate the larger aquatic animals and plants, many eggs, and detritus. A microscopic examination of the muds before the experiment showed that practically no actively growing algal forms were present. The chlorophyll contents at this time were, for all practical purposes, negligible, and were considered to be zero. For each of the stations, three of the strained mud samples and the 250 ml. of water were put into clear glass 500 ml. flasks; the remaining three samples were placed in 500 ml. flasks covered with brown wrapping paper. The purpose of the covering was to determine if any species of algae grew better in limited light. The 54 cotton-stoppered flasks, six each from the nine stations, were placed at random on a greenhouse bench, and were kept fairly near 20° C. with normal daylight as the only light source.

After one week very dense blue-green alga scums began to appear in the flasks whose contents were derived from the river mouth sediments, and at the termination of 18 days there was at least a slight growth in all the flasks. Each flask was policed to remove algae adhering to the glass and, after shaking thoroughly, a 100 ml. portion of the uniform mud and alga suspension was withdrawn from each flask for determination of chlorophyll content. A sample from each flask was examined microscopically for an identification of the species present.

Analysis of results. The results are expressed as averages for triplicate samples of the logarithms of the chlorophyll contents in mg./l. and with the analysis are given in Table IV.

The analysis of these data should be considered from two aspects. First, the mud in any sample may be capable of yielding nutrients which would support algal growth, but it may not contain any algal cells capable of inoculating the culture. Second, the mud may be incapable of supporting algal growth even though a sufficient concentration of cells are present for inoculation. These two aspects taken together are considered, in a crude way at least, to determine the overall potentiality of such a culture to produce algae.

The difference between the clear flasks and the darkened flasks is obvious and would be expected as far as the chlorophyll content is concerned, but the qualitative differences are striking in that the diatoms alone made up the bulk of the algae growing in the darkened flasks. The clear flasks contained not only more diatoms, but also much greater quantities of green and blue-green algae.

Of the bays it is quite obvious that substances in the Pheasant Branch muds initiated the greatest growths. The high values are due principally to blue-green algae.

The station differences are highly sig-

nificant with the greatest yields usually from the river-mouth muds and the least from the benthic muds, though this relationship is not constant from bay to bay.

Accordingly, the bays x station interaction is highly significant owing chiefly to the low yields from the Y 3 and U 2 sandy sediments and to the high yields from PB 1 and PB 3 cultures.

The diversities of these cultures are not surprising and experiments of Lind (1940) indicate that even greater qualitative differences might have been expected had the cultures been allowed to stand for a longer period, or had more samples been used from the same area. The identification of the blue-green algae, especially those forms known to produce blooms in Lake Mendota, is of particular interest. In general the bloom forms were found in greatest abundance in all the Pheasant Branch cultures and also in the cultures from muds of the river-mouth muds of University Bay.

Diplocystis (= *Microcystis*) *aeruginosa,* one of the most common bloom forms in Mendota, was produced by the muds from PB 1 dark, PB 2 light, some from Y 2 light, very much from U 1 light, and from U 2 light cultures. *Aphanizomenon* sp. was found in cultures of Y 3 light, PB 3 light, and U 2 light. *Gloeotrichia echinulata,* which is often a prominent bloom form in Lake Mendota, was conspicuously absent from the cultures except for possibly a few tentatively identified trichomes from Y 2 light cultures.

Of the blue-green algae not usually associated with pelagic blooms, *Oscillatoria* was present in many of the light cultures, especially in those whose sediments came from the river mouths of University Bay Creek and Pheasant Branch. At times *Oscillatoria* forms obnoxious scums locally at the river mouth areas.

The high chlorophyll values of Y 1 and Y 2 were due principally to various forms of green algae, of which *Scenedesmus quadricauda* colonies and *Ulothrix* sp. filaments are rather characteristic, and to diatoms.

TABLE IV. *Averages*[a] *of the logarithms of the chlorophyll contents in milligrams per liter of light and dark algal cultures arising after 18 days from 100 grams of sediment (wet weight) secured 11 III 49 from various locations in Lake Mendota during the ice covered period*

Source of sediment		Type of culture	
Bay	Station	Clear	Dark-ened
Yahara	River mouth, Y 1	0.2683	−0.2139
	Weedy littoral, Y 2	0.4008	−0.2173
	Benthic, Y 3	−0.2377	−0.3160
Pheasant Branch	River mouth, PB 1	0.9190	0.4836
	Weedy littoral, PB 2	0.2942	0.1527
	Benthic, PB 3	0.4169	0.1779
University	River mouth, U 1	0.3728	−0.1783
	Weedy littoral, U 2	0.1386	−0.4231
	Benthic, U 3	0.2765	−0.0626

Analysis of Variance

Source of variation	df	Mean square	F
Light	1	1.98240856	106.487**
Bays	2	1.09826719	58.995**
Stations	2	0.30479545	16.372**
Light x Bays	2	0.05093835	—
Light x Stations	2	0.09387691	5.043*
Bays x Stations	4	0.22266289	11.961**
Light x Bays x Stations	4	0.04124946	—
Error	34[b]	0.01861643	

[a] Means of logarithms of chlorophyll contents for three replicates (the variation among the three replicates is expressed under "error" in the analysis).

[b] Two degrees of freedom lost in calculation of missing values.

* Significant at 5% level.

** Significant at 1% level.

Cultures of muds taken during the spring

Procedure. To ascertain whether the muds taken beneath the ice change with respect to capabilities of initiating and supporting algal growth, the experiment just described was repeated. The sediments were obtained 21 April 1949 from the same nine stations as before, but three weeks after the ice breakup and during the spring circulation period. It was necessary, however, to determine the initial chlorophyll contents of the muds, because a considerable quantity of algae was found in the muds of the shallower regions after three weeks of ice-free conditions. The experiment was set up in the same way as previously described and the chlorophyll contents in mg./l. of the 54 flasks

TABLE V. *Averages[a] of the logarithms of the ratios of final:initial chlorophyll contents in milligrams per liter of light and dark algal cultures arising after 17 days from 100 grams of sediment (wet weight) secured 21 IV 49 from various locations in Lake Mendota during the spring circulation*

Source of sediment		Type of culture	
Bay	Station	Clear	Darkened
Yahara	River mouth, Y 1	0.7744	0.6590
	Weedy littoral, Y 2	0.6986	0.4396
	Benthic, Y 3	−0.0693	−0.2063
Pheasant Branch	River mouth, PB 1	1.4311	1.1166
	Weedy littoral, PB 2	0.2329	0.0554
	Benthic, PB 3	0.8025	0.9929
University	River mouth, U 1	0.5011	−0.0741
	Weedy littoral, U 2	−0.2768	−0.4819
	Benthic, U 3	0.7895	0.7814

Analysis of Variance

Source of variation	df	Mean square	F
Light	1	0.42741366	16.796[c]
Bays	2	1.50650923	59.202[c]
Stations	2	1.79967718	70.722[c]
Light x Stations	2	0.14232247	5.593[c]
Light x Bays	2	0.02982617	—
Bays x Stations	4	1.73640862	68.236[c]
Stations x Bays x Light	4	0.04668354	—
Error	35[b]	0.02544713	

[a] Means of logarithms of chlorophyll contents for three replicates (the variation among the three replicates is expressed under "error" in the analysis).

[b] One degree of freedom lost in calculation of missing value.

[c] Significant at 1% level.

determined after 17 days. Microscopic examination of the algae in the muds was made before and after the 17-day period.

Analysis of results. Because of the decrease in chlorophyll in some of the flasks and because of the different initial concentrations, it was necessary to express the results as ratios of final : initial concentrations. The means of the logarithms for triplicate samples are given in Table V with a statistical analysis. The negative values indicate a decline in the quantity of algae initially present so these results are not strictly comparable to those of Table IV. These declines in many of the darkened flasks and in the clear flasks containing sandy sediments from Y 3 and U 2 are somewhat complicated. It is quite possible that water action during spring circulation could remove finely divided sediments and/or algal cells from such a coarse type of substratum more readily than it would from the more consolidated fine sediments from the other stations. Data on the paucity of adsorbed cations on a sandy lake soil compared to finer soils have been given by Wohlschlag (1950).

Differences between the clear and darkened flasks were about the same as those of the preceding experiment, with the blue-greens predominating in the clear flask cultures, while the diatoms predominated in the darkened flasks.

The highly significant difference among bays was again caused by the high chlorophyll content of the Pheasant Branch stations, but University Bay had the least, whereas Yahara had the least in the earlier experiment. Blue-green algae appeared in the Yahara Bay stations after the spring turnover in increasingly greater quantities and were responsible for this shift.

The station differences, also highly significant, follow the overall pattern described for muds taken beneath the ice. The relative magnitudes of the chlorophyll contents of muds from stations within the individual bays did not compare exactly with the contents of the earlier experiment, however.

Because of the decrease in algae from Y 3 and U 2 sandy sediments, and because of the great increases from PB 1 and PB 3 substrata, the station x bays interaction is nearly identical with the former experiment.

The light x stations interaction is very significant principally because of the high increase in chlorophyll values from river mouth muds in clear flasks and because of the decrease in chlorophyll associated with sediments from the weedy littoral in darkened flasks.

To help explain some of these quantitative differences, a microscopic examination of the cultures showed that again the increases were associated with blue-green algal forms known to be bloom producers. *Diplocystis aeruginosa* was found in the

PB 2 mud cultures and *Anabaena* sp. was found in both PB 2 and PB 3 cultures. *Arthrospira* and *Oscillatoria* were found in quantity in PB 3 and PB 1, respectively. From the University Bay area, U 1 produced much *Diplocystis aeruginosa, Microcystis incerta,* and also *Anabaena* sp.; these three forms along with *Chroococcus turgidus* occurred in least quantity at U 2 and in intermediate amounts at U 3. *Rivularia* was also found in the U 3 cultures. The Yahara Bay area exhibited the greatest change between the times of the two culture experiments. The diatom prominence of Y 1 cultures of the former experiment was replaced by a prominence of blue-green forms, *Diplocystis aeruginosa, Microcystis incerta,* and some *Calothrix; Rivularia* and *Diplocystis aeruginosa* were abundant in the Y 2 cultures while in Y 3 flasks small amounts of *Coelastrum microporum,* some *Anabaena* sp., and very little *D. aeruginosa* and *Oscillatoria* appeared. There were small quantities of green algae in the Yahara Bay sediment cultures for this experiment; the greater quantities of the earlier experiment contrast sharply. Diatoms were present in all the cultures of this experiment but only in very small quantities.

Case History of an Individual *Diplocystis* (= *Microcystis*) *aeruginosa* "Bloom"

Hutchinson (1944) has stressed the importance of a succession of algal species which lead up to the summer blue-green blooms in that there is evidence of a correlation between the chemical nutrients or growth substances which are left over or released by one stage of the succession and which affect the following stage. He noted that blue-green blooms appear when the level of nutrients is relatively low. The sequence of events in Lake Mendota during the spring of 1949 suggests a possible application of this explanation to a light bloom of *Diplocystis aeruginosa* on 3 June 1949.

On 30 March 1949 the ice cover of the lake broke up. A diatom irruption dominated by *Asterionella* was initially evident. With the decline of diatoms the lake became the clearest on record. On 12 May the Secchi disc transparency was 9.5 m. at which time the chlorophyll contents of the waters were very low (see Tables I and II), due chiefly to small quantities of a green alga, *Chlorella* or *Palmellococcus.* On 1 June, a stormy day, the chlorophyll analyses for three pelagic stations were 10.5, 9.5, and 10.0 mg./cu.m., respectively, and the Secchi disc reading was 5.0 m. These quantities of chlorophyll were due principally to *Melosira, Cosmarium,* and *Ankistrodesmus.* A few scattered cells of *Diplocystis aeruginosa,* not evident as a surface scum, occurred throughout the lake, but locally at littoral stations Y 2 and PB 2 there were, respectively, 10,200 and 32,600 colonies per liter. No colonies were found elsewhere. (Note that the muds from the Pheasant Branch region yielded good cultures of this species several weeks earlier.) All colonies found were bright blue-green and less than 70 microns in diameter. On 2 June, a calm day, the lake had a slightly turbid appearance, not in the least indicative of blooming. The lake definitely bloomed on 3 June. Open water scums were due to *D. aeruginosa* at 32,460 colonies per liter with a diameter of 0.2–1.5 mm. Of this volume of water it was estimated that there were 40–50 aggregations of cells whose average diameter was about 5 mm. A relatively low chlorophyll content of 21 mg./cu.m. on 4 June indicated that these persisting blue-greens have little chlorophyll when compared to values for green algae of similar dimensions. The very small bright blue-green colonies observed on 1 June possessed very little gelatinous sheath material; the 4 June colonies had thousands of smaller cells, were pale green, and had relatively great masses of gelatinous material.

If the chlorophyll content is even a rough indication of the physiological activity of the cells (and a rough measure

of their requirements for nutrient materials), the slow increase in chlorophyll and the rapid increase in bulk could be explained on the basis of release of a relatively low concentration of nutrients, perhaps undetectible chemically, from the sediments at a time when the succession of preceding algal forms had set the stage for the appearance of the blue-green species. That organic and inorganic substances other than P, N, and Si compounds are necessary for algal development, has been suggested by Hutchinson (1944). The importance of sediments as a source of these other nutrients may be indicated by the fact that many experimental cultures of algae are enhanced when soil extracts are added to the synthetic media (Chu 1942; Rodhe 1948).

General Appraisal

The value of the chlorophyll content measurements of natural waters depends upon completeness of removal of algae, completeness of chlorophyll extraction, evaluation of extract color in quantitative terms, and the relationship of chlorophyll content to the quantity of algae *per se*. Critiques of pigment extraction methods and their applications have been presented by Harvey (1934), Gardiner (1943), and Tucker (1949).

The filtration of algal cells from the water samples was regarded as complete, since practically no algae would appear in the filtrates which were allowed to stand as nonsterile culture media for several weeks. Extractions by methyl alcohol have certain advantages for pigments of fresh-water algae (Gardiner 1943), and these extractions were regarded as complete because periodic re-extractions of the contents on the filter papers showed that in no case was any detectible pigment left on them after the initial 24-hour extraction. While the concentration of pigment was measured only with the use of the 660 millimicron filter in the Evelyn colorimeter, it was believed that this procedure gave at least a fair indication of the chlorophyll-a, a pigment common to all the more abundant algal species. The other common pigments, xanthophyll and carotin, could not be detected accurately due to interference by yellowish coloring matter derived from detritus in the water or from the sediments. In this connection it was encouraging to note that the yellowish extracts from algae-free sediments gave no indication of chlorophyll when the 660 millimicron filter was used.

That the chlorophyll content of a water sample is at best a proximate determination of algal cell content must be emphasized, though chlorophyll contents did agree with the many cell counts made, at least in a semiquantitative manner. On the other hand, cell counts in themselves do not necessarily give an indication of the photosynthetic activity. Furthermore, quantitative comparisons among cell, filament, or colony counts of unlike species appear to be impracticable. Chlorophyll contents do give some indication of the photosynthetic activity of the algae, and though nonspecific they are comparable.

The data on distribution of algae as measured by the chlorophyll contents of pelagic waters over three major depressions in Lake Mendota show definitely that any differences among these areas must be due only to random variation, on the basis of collections at approximately one-month intervals for nearly one year. It is quite likely that differences among pelagic areas and between the surface and 10 m. levels would exist over shorter periods, however. The fluctuations of chlorophyll contents correspond quite well with the phytoplankton counts of Birge and Juday (1922) on both a seasonal and intraseasonal basis. Especially significant is the great temporal variability in algal abundance at a given collecting area. Likewise temporal variability was significantly omnipresent even when controlled experiments were carried out within a period of a few weeks. Some of this variability could probably be accounted for if a better scheme of breaking the year up into seasons or stages could

be instituted using some criterion other than the state of thermal stratification. Hutchinson (1944) used stages of algal succession. In Lake Mendota the stages of algal succession, in part, have not been constant from year to year. A case in point is the presence of several blooms of blue-green algae one year and their absence the next. Unfortunately, at the present time not enough information exists to indicate whether a given blue-green species blooms at a definite successional stage in the summer or whether it occurs at a time with no relation to the succession of other biological events. In the latter instance environmental, rather than successional, phenomena may hold the key to the explanation of the Myxophyceaen blooms.

In the comparisons of the three bay areas the consistent individuality which some of the stations within the bays exhibited looms large as an important factor associated with the possibility of a localized origin of blue-green blooms. Such individuality is emphasized even more when it was observed to be persistent through some of the seasonal changes. Furthermore, on the basis of general qualitative observations over the entire lake, it is believed that such individualities are the rule for littoral areas.

The fact that the three weedy littoral areas studied did not have the same relative amounts of algae as compared to the stations adjacent to them provides an interesting example of station individuality. Only the weedy areas of University Bay seem to have low chlorophyll contents such as would be expected if the antagonistic effect of large aquatic plants were operating as they did in the experimental ponds of Hasler and Jones (1949). While organic substances derived from higher plants have been postulated by Schreiter (1928) as inhibitors of algal growth, there is yet no direct proof that such substances exist. Other explanations of the antagonism between higher plants and algae suggested by Hasler and Jones are competition for soluble nutrient materials and shading effect of the larger plants. Experiments by Pond (1903), Roelofs (1944), and Wohlschlag (1950) have shown that many of the higher rooted plants depend principally upon the substratum and not the water for nutrients. If shading of the water by the aquatics were to reduce algal development, this effect would be expected to apply to plant areas generally, and such a situation did not appear to exist in the three areas studied in Lake Mendota.

The mud culture experiments offer another possible explanation of the diversities and sources of both nutrient materials and algal cells potentially able to initiate algal growth, and especially growth of bloom-forming blue-green algae. Lind (1940) emphasized the property of various sediments to differ quantitatively and qualitatively and noted that the anaerobic cultures tended to produce more Myxophyceae. As far as the production of blue-green algae is concerned, Lake Mendota mud culture experiments, in which the production of algae in flasks aerated by shaking several times daily was compared to the production in more anaerobic unshaken flasks, showed no statistical difference. Mortimer (1941–1942) and Hutchinson (1941) discussed in detail some of the mechanisms by which nutrient materials may be released from the muds and circulated in the lake waters as have Hasler and Einsele (1948) in regard to the liberation of iron and phosphorus.

That the marginal algae of ponds varies with the sediments and that the wind may play an important part in distributing both algae and mud-derived nutrients has been considered by Lund (1942). Some evidence of this sort can be given for Lake Mendota on the basis of chlorophyll determinations and microscopic examinations of shore waters at Picnic Point and near Fox's Bluff on opposite sides of the lake (see Fig. 1). During the months of June and July in 1948 six series of eight water samples, four from each shore, were taken. For five of the six series the Fox's Bluff shore samples were obtained

after that shore had been exposed to wave action due to easterly or southerly winds for at least 48 hours. The chlorophyll contents of the 20 samples from the Fox's Bluff wind-exposed area averaged 20.5 mg./cu.m. as compared to the 20 samples from the relatively calm Picnic Point waters which averaged 12.4 mg./cu.m. For the one series when the Picnic Point region was wind exposed for at least 48 hours, the four samples on this side of the lake averaged 15.0 mg./cu.m. as compared to the average of four samples from the calmer Fox's Bluff shore which was 9.1 mg./cu.m. A microscopic examination of these water samples indicated that both floating and suspended algae were more numerous on the wind-exposed shores.

If wind-induced turbulence of the waters were associated directly or indirectly with the promotion of algal growth, several plausible explanations may be hypothesized. First, the sediments of the shallower waters may be stirred up, releasing chemical nutrients, and exposing sedimented algal spores and other potentially reproductive structures. Second, the turbulence of the surface waters may induce circulation in the supposedly summer-stagnated hypolimnion which could release nutrients derived there to the nutrient poor surface waters; data are needed on this point to help explain, for example, whether the potentially productive muds beneath Pheasant Branch Bay could contribute to algal production in the lake. These two explanations would seem to have a sound basis in terms of circulation of Lake Mendota waters as worked out by Bryson and Suomi (1950). Third, it is possible that turbulence of waters may result in exposure of the existing algal cells to more water with potential nutrients even if these nutrients are at a low level per unit volume of water, though a series of experiments designed to examine this point yielded negative results. Finally, it is possible that a concentration of algae can take place independent of local growth conditions but dependent entirely upon the nature of the settling velocities of the algae and upon the nature of the natural convection cells occurring in a body of water (Bryson and Suomi 1950; Stommel 1949).

Summary

1. Differences in quantities of algae for widely differing areas of Lake Mendota are very pronounced both seasonally and intraseasonally. Differences are likewise prominent in experiments extending over periods as short as several weeks.

2. Different bay areas and the stream mouth, weedy littoral, and pelagic stations within these bays have characteristic quantities of algae. Certain of the individual stations have characteristics retained from one season to the next; others vary greatly on a seasonal basis. In any case, where station individuality is indicated, it is present over and above temporal variation.

3. Cultures of algae derived from sediments obtained in the winter and in the spring exhibited characteristic differences from bay to bay and from station to station within the bays. In a general way, the same station individualities present in the cultures were present in corresponding collections from overlying waters. Coarse, sandy sediments from the same locale produced more algae when obtained before the ice-free spring circulation period. Prominent blue-green species which appeared in these cultures are mentioned and their possible significance to subsequent blooms in the lake is discussed. The pattern of distribution of agents causing production of algae should be examined within the sediments of the entire lake.

4. In Lake Mendota there is a suggestion that algal concentrations are greater at a littoral area after a 48-hour exposure to onshore winds than at a similar area not so exposed.

5. A study of chlorophyll, chemical, and microscopic data suggests that the sudden appearance of numerous large colonies of *Diplocystis* (= *Microcystis*) *aeruginosa*

comprising a bloom is accompanied by an increase in gelatinous matter which is proportionately greater than the increase in physiological activity as represented by an increase in chlorophyll.

6. On the basis of ecological observations of Lake Mendota and exploratory experiments, the hypothesis of wind produced agitation of sediments is discussed as a possible agent in the initiation and promotion of blue-green blooms in relation to the seasonal succession of algal blooms.

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SOME EFFECTS OF LIVESTOCK GRAZING ON PONDEROSA PINE FOREST AND RANGE IN CENTRAL WASHINGTON [1]

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Many stories have arisen to describe what the vegetation of the virgin ponderosa pine forest and range was like before white man, his grazing animals, and logging machinery began to harvest the forest land crops. Are the tales of an open, parklike tree overstory with dense stands of grass true? If so, what has caused the change to the present thin stands of grasses and dense stands of advance tree reproduction? It is difficult to answer these questions correctly, for practically all of the ponderosa pine forest has been used in some degree by white man.

One of the few relicts of virgin ponderosa pine forest and range, which provides an opportunity to investigate the original appearance of the type, is Meeks Table in central Washington. Meeks Table is a 70-acre isolated plateau that has never been grazed by livestock because natural barriers have made it inaccessible. Meeks Table was set aside by the U. S. Forest Service as a Natural Area in 1948. As such it will never be logged or grazed by livestock, but will be maintained in its natural state for observation and study. For comparison, there is Devils Table, a larger plateau covering approximately 2,000 acres four miles southeast of Meeks Table. Devils Table is essentially similar to Meeks Table in geologic origin, elevation, climate, and timber type, but Devils Table has been heavily utilized by livestock during the past 40 years. Both tables are ponderosa pine forest areas which have never been logged.

Data were gathered from Meeks and Devils Tables in 1947 and 1948 on the herbaceous and shrubby vegetation, the tree reproduction and overstory, and the soils. This paper reports the results of the study.

LITERATURE REVIEW

Literature on the original appearance of the ponderosa pine forest range type is scarce. Nor do many references exist which clearly explain changes from sparse to dense ponderosa pine reproduction in the uncut pine forest. However, there are some references which relate to the Meeks Table-Devils Table study.

Arnold (1950) reported that herbaceous plant cover in ponderosa pine forests in northern Arizona has been markedly affected by logging and grazing. The forest in 1901 and 1902 had a deficiency of seedling and sapling pines and was more fully occupied by herbaceous species than today. However, a general abundance of young pines has become established over extensive areas, principally from a 1919 seed crop. These pines have caused reduction in perennial grass density independent of any livestock grazing influence. Herbaceous density and harvested grass yields declined under increasing amounts of pine canopy. Bunchgrasses suffered their greatest losses in heavily grazed forest openings and under lighter pine canopies, and grass species more resistant to grazing damage increased in density on a grazed area. There were more perennial weeds and annuals where heavy grazing had reduced all perennial grass species, but loss in forage production due to the influx of

[1] The author is indebted to Ellerslie W. Stevenson, Quentin Jones and Rex S. ZoBell for assistance in collecting the data, and to Robert F. Tarrant for doing the soils textural analyses. With the exception of textural analyses, all laboratory analyses on soils were made by the National Bureau of Standards, Seattle, Washington Laboratory.

young pine stands was accompanied by few changes in herbaceous composition.

Weaver (1943, 1947) has theorized that dense stands of stagnating ponderosa pine reproduction have developed largely because of total fire exclusion. In a later paper Weaver (1950) stated that overgrazing has been of great significance in development of abnormally dense stands of pine reproduction through breaking up of original sod cover and preparation of mineral seedbeds. He indicated that the development of dense stands of reproduction has resulted in forage plants being crowded out of the forest environment.

Hill (1917) surmised that grazing had a neutral effect upon germination and early establishment of pine reproduction. He suggested that grazing had an important effect in removing inflammable material and in reducing destruction of reproduction by fire.

Gardner (1950) found grass density on upland desert grassland in New Mexico 110 per cent higher on an area protected from grazing for thirty years than on an adjacent grazed area. However, he found little difference in species composition between the two areas. Laboratory analysis of upland soils showed no critical differences between the soil under protection from grazing and that not protected from grazing.

Methods

Density and composition of the herbaceous and shrubby understory vegetation on Meeks Table and Devils Table were determined by the square-foot density method (Stewart and Hutchings 1936), on sixty-nine plots 100 square feet in area spaced mechanically from randomly chosen starting points. Forty-one plots were sampled on Meeks Table and 28 on Devils Table. Herbage production of

Fig. 1. Looking west to Meeks Table in the center background. The only means of access to this isolated plateau is an extremely steep game trail which winds up a knife-like ridge at the west end of the Table. FS Photo 449657 (1947).

FIG. 2. Pinegrass forms an almost unbelievably lush mat on Meeks Table. It grows from the immediate bases of the trees out into the grassland openings on the deeper soils. FS Photo 459737 (1948).

pinegrass (*Calamagrostis rubescens*) was determined from 10 clipped samples from each Table, collected and air-dried. Plots from which pinegrass was clipped each contained 9 square feet. Trees less than 4 inches dbh (diameter breast high) were tallied by species and height class on the plots 100 square feet in area. Data on tree overstory were recorded on sixty-nine $\frac{1}{10}$-acre plots. All trees 4 inches dbh and over were tallied by species and dbh class. Total crown density was ocularly estimated above each $\frac{1}{10}$-acre plot. Diameters were estimated with checks by diameter tape. Observations were made on wildlife, rodents, insect damage to trees, and other pertinent factors.

The plots were grouped for analysis according to three general type classifications: (1) pinegrass-elk sedge (*Carex geyeri*) understory; open ponderosa pine (*Pinus ponderosa*) overstory; (2) pinegrass-elk sedge understory, mixed ponderosa pine-common Douglasfir (*Pseudotsuga taxifolia*) overstory; and (3) subalpine needlegrass (*Stipa columbiana*)-Sandberg bluegrass (*Poa secunda*) open grassland type.

The soils on both Meeks and Devils Tables were sampled by digging pits in representative locations in the general vegetative types, and describing the soil profile, texture, structure, litter, drainage, and other factors. Samples were collected from each horizon of each pit; these samples were later analyzed in the laboratory for pH, moisture equivalent, total nitrogen, potash, phosphoric acid, total organic matter, and per cent of sand, silt, and clay.

A grassland type occurring in a narrow band around part of the exposed edge of Meeks Table was not sampled. This type

was covered with unconsolidated basalt. No complete soil description was made of this area.

All plant nomenclature is according to Standardized Plant Names (1942). The taxonomic authority is added to each animal name.

General Features of the Tables

During Pliocene time, water eroding what is now the Rattlesnake Drainage of Yakima County, Washington, separated Meeks Table from the surrounding terrain. Subsequent erosion has left Meeks Table a seventy-acre, isolated, gently sloping basalt-capped plateau. It is immediately surrounded by precipitous 200 to 300 foot cliffs and stands about 1,000 feet above the base levels of the adjacent drainages (Fig. 1). The top of Meeks Table can be reached only by traversing a narrow and extremely steep, infrequently used game trail which winds up a narrow, knife-like ridge at the west end of the Table. Although the geologically similar but grazed plateau, Devils Table, is bounded on two sides by high cliffs, livestock have had easy access on the other two sides of this plateau.

Meeks Table is capped by basalt, largely dense dark trap and diabase, the diabase predominating among the rocks exposed. Devils Table appears to be geologically similar. The high point of each Table is about 4,500 feet above sea level. Each slopes to the northeast at a rate of 10 per cent.

The climate in this ponderosa pine zone is typically continental with hot and relatively dry summers and cold, wet winters. Annual precipitation may average 20 to 25 inches with much of it occurring in the form of winter snows.

Rocky Mountain mule deer (*Odocoi-*

Fig. 3 The predominant ground cover on Meeks Table, even in the grassland openings, is pinegrass and elk sedge on the deeper soils. Notice the almost complete lack of any tree reproduction. FS Photo 449659 (1947).

FIG. 4. Ponderosa pines are advancing into grassland openings on Devils Table. FS Photo 449671 (1947).

leus hemionus macrotis Say) and black bear (*Euarctos americanus altifrontalis* Elliot) were part of the native fauna of the surrounding lands. Rocky Mountain elk (*Cervus canadensis nelsoni* Bailey) were introduced to the lands near the two Tables in 1913 and are now abundant. All of these animals occasionally visit Meeks Table, even though there is no permanent water supply, and they probably reside yearlong on Devils Table. A small population of rodents, including pocket gophers and mice, is resident to Meeks Table.

RESULTS OF THE STUDY OF THE TWO TABLES

Herbaceous and shrubby vegetation

In 1947, the herbaceous understory vegetation was luxuriantly thick on ungrazed Meeks Table. Shrubs were of minor importance. Elk sedge, Wheeler bluegrass (*Poa nervosa*), lupine (*Lupinus* spp.), and some other herbaceous species grew there, but the striking thing about this vegetation was the great density of pinegrass. Pinegrass grew luxuriantly and vigorously and formed a dense covering over all the deeper soils, even out into the grassland openings (Fig. 2). While grassland openings on grazed Devils Table had been invaded by ponderosa pine, the grassland openings on ungrazed Meeks Table lacked pine reproduction (Figs. 3 and 4).

The density of herbaceous and shrubby vegetation beneath open ponderosa pine averaged 35 per cent on Meeks Table and 14 per cent on Devils Table (Table I). In this type, pinegrass made up two-thirds of the herbaceous and shrubby vegetation on Meeks Table; on Devils Table it made up only one-third of the understory vegetation (Fig. 5). In 1948, pinegrass beneath open ponderosa pine

TABLE I. *Average per cent densities of the herbaceous and shrubby vegetation on Meeks Table and Devils Table by species and vegetative type in 1947*

Species	Open ponderosa pine; Pinegrass-elk sedge		Mixed ponderosa pine-Douglasfir; Pinegrass-elk sedge		Grassland
	Meeks Table	Devils Table	Meeks Table	Devils Table	Meeks Table
Grasses and sedges					
Agropyron spicatum		1.0			
Bromus marginatus	0.1		T[1]		0.2
Calamagrostis rubescens	22.3	4.4	12.7	5.5	T
Carex geyeri	5.6	1.7	2.3	2.6	0.2
Carex rossi			T		0.1
Danthonia intermedia	0.2		0.5		
Danthonia unispicata					0.8
Festuca idahoensis	0.2	1.5			0.9
Festuca occidentalis			0.1	T	
Poa nervosa	1.0	0.5	0.5	T	0.2
Poa secunda		0.4			3.6
Sitanion hystrix	0.1	T			0.1
Stipa columbiana	0.2				5.3
Totals, grasses and sedges	29.7	9.5	16.1	8.1	11.4
Forbs					
Achillea lanulosa	0.2	0.3	T	0.3	0.1
Anaphalis margaritacea	T				
Antennaria luzuloides	0.5	0.1	0.1		
Antennaria rosea				0.1	
Arnica cordifolia	0.1		0.2		
Aster spp.				T	
Astragalus spp.		0.3			
Balsamorhiza sagittata	0.5		0.1		0.7
Calachortus macrocarpus			T		
Collomia spp.					T
Draba spp.					T
Eriogonum spp.					T
Eriophyllum lanatum					0.2
Frasera speciosa	0.1		0.5	0.2	
Gayophytum spp.					0.2
Hieracium chapacanum	0.7	0.2	0.4	0.3	0.2
Lithospermum ruderale		0.1		0.1	
Lomatium spp.					T
Lupinus spp.	1.8	1.0	1.3	2.8	
Madia glomerata			T		0.9
Penstemon spp.			0.1	T	0.2
Phlox spp.	0.9	0.1	0.6		0.4
Potentilla gracilis			T		
Sedum douglasi	T	T			0.4
Sieversia ciliata	0.4		T		
Zygadenus spp.		T			
Totals, forbs	5.2	2.1	3.3	3.8	3.3
Shrubs					
Amelanchier florida			T		
Arctostaphylos nevadensis		2.2	1.1		0.4
Artemisia rigida	0.1				4.9
Holodiscus discolor			0.6		
Pachistima myrsinites			T		
Purshia tridentata		T	0.1		
Salix spp.	0.1		0.6		
Spiraea lucida			0.3	0.2	
Totals, shrubs	0.2	2.2	2.7	0.2	5.3
Totals, all understory vegetation	35.1	13.8	22.1	12.1	20.0

[1] Trace.

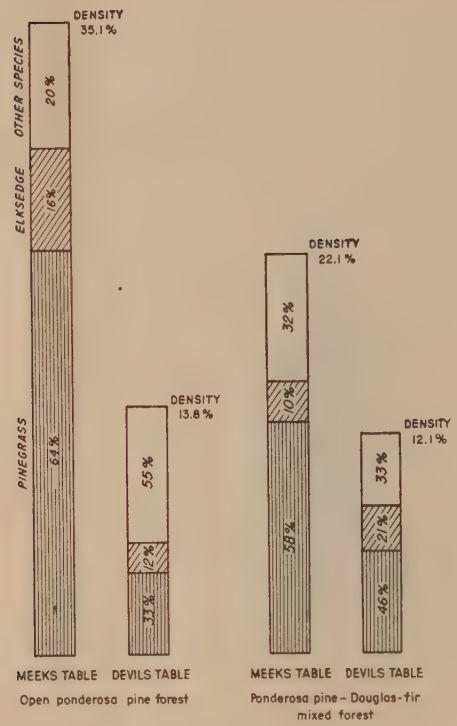

FIG. 5. Density (per cent of ground covered) and composition of herbaceous and shrubby vegetation on Meeks Table and Devils Table in pinegrass-elk sedge type in 1947.

produced 850 pounds of air-dry herbage per acre on Meeks Table against only 240 pounds on Devils Table.

Pinegrass also dominated the vegetation beneath the mixed ponderosa pine-Douglasfir forest on Meeks Table, but it made a cover somewhat less dense than it did under the open pines. In this more shady environment, the average total density of the herbaceous understory vegetation was 22 per cent of which pinegrass made up a little more than one-half. On Devils Table in the mixed ponderosa pine-Douglasfir forest type, the average total density of herbaceous understory vegetation was 12 per cent, with pinegrass making up just a little less than one-half.

Elk sedge was subordinate to pinegrass on both Meeks and Devils Tables, but the densities of the two species were much closer together on Devils Table. Devils Table supported only a little over twice as much pinegrass as elk sedge, while Meeks Table had from four to six times more. In the open ponderosa pine type, pinegrass density on Devils Table was only one-fifth as great as pinegrass density on Meeks Table; elk sedge density on Devils Table was one-third of elk sedge density on Meeks Table. In the ponderosa pine-Douglasfir mixed forest type, pinegrass density on Devils Table was two-fifths as great as pinegrass density on Meeks Table, while elk sedge density on Devils Table was slightly greater than elk sedge density on Meeks Table.

Densities of total understory vegetation, elk sedge, and pinegrass proved significantly different between the two Tables in the timber types in all but one comparison. The density of elk sedge on Devils Table was slightly higher than the density on Meeks Table in the ponderosa pine-Douglasfir type. In all other comparisons, densities were lower on Devils Table. Densities of pinegrass and elk sedge were significantly correlated in the timber types on both Tables.

The number of species in the understory vegetation making up densities on the two Tables provided interesting comparisons. In the open ponderosa pine type, there were 19 species on ungrazed Meeks Table and 14 species on grazed Devils Table. In the ponderosa pine-Douglasfir mixed forest type, there were 18 species on Meeks Table and but nine on Devils Table.

Open grassland occupied 7 acres on Meeks Table. The grassland contained soil hummocks 4 to 15 feet in diameter projecting 4 to 8 inches above the level of the adjoining depressed ground. Both the hummocks and the depressed ground between them supported a high density of grasses on Meeks Table. Subalpine needlegrass made up almost 30 per cent of the vegetation while it and other grasses made up 62 per cent of the total vegeta-

tion. Average total density was 20 per cent. On some of the hummocks, vigorous stands of pinegrass grew together with some elk sedge. The composition of vegetation on the larger areas of swales, or depressions between the hummocks, was much different than the hummocks' vegetation. Subalpine needlegrass, Sandberg bluegrass, onespike danthonia (*Danthonia unispicata*), stiff sagebrush (*Artemisia rigida*), and cluster tarweed (*Madia glomerata*) grew in the swales. Dried foliage of ephemerals in the swales denoted a weedy cover in the spring. Although there was a grassland type on Devils Table, it was not comparable to the hummocked grassland of Meeks Table.

Sampling and reconnaissance showed scattered plants of antelope bitterbrush (*Purshia tridentata*), creambush rockspirea (*Holodiscus discolor*), willow (*Salix* spp.), cherry (*Prunus* spp.), and some other shrubs occurring on Meeks Table and less abundantly on Devils Table, but they had been heavily utilized by transient deer and elk on both Tables. Elk sedge had been heavily utilized while pinegrass was only slightly used on Devils Table when the area was sampled. Leaf tips of some elk sedge plants had been grazed by game on Meeks Table but pinegrass had not been grazed.

Timber

The timber overstory on Meeks Table (Fig. 6) consisted of an open stand of pure ponderosa pine in mixed age groups and some groups of mixed ponderosa pine-Douglasfir with an occasional large western larch (*Larix occidentalis*) and grand fir (*Abies grandis*) (Table II). The timber overstory was similar on Devils Table but there were a few more Douglas-

FIG. 6. A predominantly open ponderosa pine type with interspersed grassland areas covers most of the top of Meeks Table. Two of the striking things about the plant cover shown in this photograph are the almost complete lack of tree reproduction and the great density of grasses. FS Photo 449660 (1947).

TABLE II. *Number of trees (4 inches dbh and larger) per acre in timber stands on Meeks Table and Devils Table by diameter groups for each species*

Diameter group dbh, inches	Ponderosa pine		Common Douglasfir		Western larch		Grand fir	
	Meeks Table	Devils Table	Meeks Table	Devils Table	Meeks Table	Devils Table	Meeks Table	Devils Table
4–12	14	18	15	22	(0.2)	5	1	1
14–28	14	16	3	4	(0.2)	0	0	0
30 and over	2	5	0	1	0	1	0	0

firs and western larches. Meeks Table was classed a low site IV for ponderosa pine while Devils Table was classed site V by the Forest Survey.[2]

One of the most striking differences between the two Tables was the almost complete lack of tree reproduction on Meeks Table (Fig. 6) compared to a much denser stand of reproduction on Devils Table (Fig. 7). On Meeks Table, the timber stand was open and parklike, and there were only 85 trees per acre less than four inches dbh. But there were 3,291 per acre on grazed Devils Table (Table III). Sampling on Meeks Table recorded no reproduction of ponderosa pine although reconnaissance showed several young pines. There were 2,033 small ponderosa pines per acre on Devils Table. On parts of Devils Table as many as 300 ponderosa pine trees about forty years old grew on each of several $\frac{1}{10}$-acre plots.

Examination of increment cores from trees with fire scars showed that no fires had burned over the entire top of Meeks Table in any one year during the past 125. Fires on individual trees were dated to have occurred in 1814, 1834, 1840, 1862, and 1898, but no ring damage for any one year was common to all trees. One tree showed ring damage in both 1834 and 1862, indicating probable fires in both of these years. Devils Table probably has had a similar spotty fire history. Increment cores indicated fires there in 1810, 1831, and 1882. All of these apparently light ground fires.

Crown densities of the timber overstories were practically the same on Meeks and Devils Tables. In the open pine type, tree crowns covered 10 per cent of the ground on Meeks Table, and 12 per cent on Devils Table. In the mixed pine-Douglasfir type, crowns covered 27 per cent of the ground on both Meeks and Devils Tables.

Soils

Soils beneath the timber showed some differences between Meeks and Devils Tables. On Meeks Table, the litter and humus of pinegrass and pine needles beneath both forest types made a spongy, mull humus cushion 1½ to 2 inches thick which overlay a thin podsolized layer. The well-developed A horizons extended to depths of from 8 to 11 inches and were dark brown, friable, coarse sandy loam to loam soils with crumb structure

TABLE III. *Number of trees (less than four inches dbh) per acre by species in timber stands on Meeks Table and Devils Table*

Species	Meeks Table	Devils Table
Ponderosa pine	0	2,033
Common Douglasfir	0	1,016
Western larch	0	242
Grand fir	85*	0
Totals	85	3,291

* Based on eight seedlings which grew on one of 41 sample plots.

[2] From statistics of the Inventory Phase of the Forest Survey, Pacific Northwest Forest and Range Experiment Station, 1936. In the Pacific Northwest, the site quality of ponderosa pine region forest lands bearing mature timber crops is judged by the average height of the mature dominant trees: Site IV: total height at 100 years = 79 feet; total height at maturity 114 feet. Site V: total height at 100 years = 65 feet; total height at maturity 89 feet.

and with pH's ranging from 5.6 to 5.3. The brown B horizons extended to about 18 inches below the soil surface. They ranged from coarse sandy loam to a gritty clay with strongly developed nut structure; the clay showed colloidal staining on the cleavage surfaces. The B horizons had pH's ranging from 5.5 to 4.7. An unusual, black, waxy, fragmental clay containing many fine roots and having an extremely high moisture equivalent of 59.5 per cent appeared at 18 inches on part of Meeks Table. The total organic matter of this clay was only 2.4 per cent. Occasional iron stains were oxidized red in this clay. Its pH of 4.7 was the most acid of all the samples.

On Devils Table the litter and humus were one to two inches thick, but they did not have the spongy character evident on Meeks Table. Devils Table soils contained the shallow podsolized layer just beneath the organic matter, but they did not show the black, waxy clay. Top soils on timbered areas of Devils Table were coarse, medium, and fine sandy loams underlain by coarse sandy loam to clay loam subsoils. Soil acidity in the A horizons of Devils Table averaged 5.6 expressed in pH, or about the same as on Meeks Table; the 5.8 pH of Devils Table's B horizon was somewhat higher than the 5.1 pH of the B horizon on Meeks Table (Table IV).

The soils of the grassland areas on Meeks Table were more rocky than the soils under timber. Soils hummocks generally displayed a sparse litter but were bare in some places. No humified litter existed. A 6-inch, gray-brown A horizon overlay a 12-inch, light-brown B horizon. The A horizon was a moderately developed, friable, medium sandy loam with crumb structure and a pH of 5.9. The

FIG. 7. This site on Devils Table is representative of the abundant ponderosa pine advance reproduction growing there. While most of the ponderosa pine forest ranges in eastern Washington and Oregon support equally abundant stands of ponderosa pine reproduction, many ranges have even thicker stands of young pines. FS Photo 449670 (1947).

TABLE IV. *Averages of chemical and mechanical analyses of Meeks Table and Devils Table soils*

Analysis	Timber sites A horizon		Timber sites B horizon		Grassland sites Meeks Table only	
	Meeks Table	Devils Table	Meeks Table	Devils Table	A horizon	B horizon
pH	5.4	5.6	5.1	5.8	5.9	5.7
Moisture equivalent (%)	21.5	24.5	37.3	19.9	18.5	16.2
Total nitrogen (%)	0.16	0.15	0.12	0.09	0.22	0.16
Total organic matter (%)	5.3	4.5	3.1	2.2	4.4	2.6
Available potash (ppm)	343	465	267	395	260	135
Available phosphoric acid (ppm)	78	108	36	72	23	14
Textural class	Coarse sandy loam to loam	Coarse sandy loam to fine sandy loam	Coarse sandy loam to clay	Coarse sandy loam to clay loam	Medium sandy loam	Medium sandy loam to loam

B horizon was a compact medium sandy loam to loam with a pronounced nut structure, pH of 5.7, and a slight amount of lime. The cleavage planes of the B horizon showed colloidal staining. At approximately 18 inches below the soil surface numerous diabase rocks appeared.

Only three soil samples out of nineteen on both tables tested 0.2 per cent nitrogen or better. These occurred beneath open pine timber and grassland. The highest amount of phosphoric acid was only 170 ppm and phosphorus values ranged down to 12 ppm. Individual potash values ranged from a high of 620 ppm in an A horizon of the open pine type on Devils Table to a low of 90 ppm in a B horizon of the grassland type on Meeks Table.

DISCUSSION

Data obtained in this study support the belief that parts of the virgin ponderosa pine forest in eastern Washington and eastern Oregon were open and parklike with dense stands of grass beneath the timber.[3] The data also provide some valuable clues to the composition and density of herbaceous understory vegetation on top-condition ponderosa pine range. This information should be useful in range condition classifications. Meeks Table can be considered representative of top-condition ponderosa pine forest range with a pinegrass understory. As such it can be a top standard against which many other pine forest ranges with similar climate and physiography can be compared.

Perhaps equally important to the enlightenment on what the virgin conditions were is the evidence produced that pine forest range in top condition may actually complicate pine silviculture. Attainment or maintenance of litter and vegetative ground cover of densities and compositions comparable to those on Meeks Table may prevent establishment of adequately-stocked stands of advance tree reproduction. Pearson (1923) has indicated that deep accumulations of litter were not favorable to good pine germination. For best management of ponderosa pine forest and range lands, it may not be desirable to achieve densities of herbaceous understory vegetation as high as those on Meeks Table. Less dense cover may be desirable.

Data from ungrazed Meeks Table suggest a plant composition concept contrary to one commonly accepted. Some in-

[3] In the Pacific Northwest, pinegrass, bunchgrass, bitterbrush, sagebrush, and other shrub understories are found beneath pine timber. Observations and preliminary study support the hypothesis that each of these groups is a separate vegetative subtype. The Meeks Table-Devils Table data apply to that part of the ponderosa pine forest range which is commonly called pinegrass subtype.

vestigators have held that the amount of elk sedge was much greater than pinegrass in the virgin ponderosa pine forest range. Because elk sedge is commonly more palatable to livestock than pinegrass, the theory has been advanced that elk sedge was reduced in density more rapidly than pinegrass by high intensities of livestock grazing, and pinegrass became dominant. Meeks Table data do not support that theory. The data suggest that elk sedge may have been subordinate to pinegrass in the virgin ponderosa pine forest range: four to six times more pinegrass than elk sedge grew on ungrazed Meeks Table.

Meeks Table had a richer vegetation than the grazed Devils Table. Several forb and shrub species which are recognized as good forage plants occurred on Meeks Table but were absent from areas sampled on Devils Table. Heavy grazing use on Devils Table may have removed them from the flora there.

A greater difference in total density of understory vegetation between Meeks Table and Devils Table occurred in the open ponderosa pine type than in the more heavily canopied ponderosa pine-Douglas-fir type. The natural preference of livestock to graze in the open may account for this. The open pine areas of Devils Table may have received heavier grazing use than the pine-fir type.

Highly significant relationships existed between crown density of the timber overstory and densities of total understory vegetation, pinegrass, and elk sedge in the timbered types on Meeks Table. As shading by tree canopies increased, amounts of understory vegetation decreased. No significant relations existed between crown density and these densities of understory vegetation on Devils Table. This lack of relation on Devils Table may possibly have been due to heavier grazing use in the open pine areas. The stand of advance tree reproduction on Devils Table influenced densities of understory vegetation. Analysis showed there was no correlation between crown density of overstory and number of young trees on Devils Table. Since the reproduction stands were about as dense under heavy overstory canopies as under light canopies, the amount of competition given the herbaceous understory vegetation by tree reproduction probably was of comparable intensity over the entire sampled area. This competition factor appeared more important in influencing growth of total herbaceous vegetation, and pinegrass and elk sedge on Devils Table, than was any influence from the canopies of trees in the overstory.

Density of understory vegetation and number of small trees on grazed Devils Table were not significantly related. However, this lack of significant relationship on Devils Table does not invalidate the theory that the dense understory vegetation was responsible for the lack of advance tree reproduction on Meeks Table. The density of understory vegetation on Devils Table was significantly less than the density on Meeks Table. Furthermore, because of heavier grazing pressure on Devils Table thirty to forty years ago, the density of the understory vegetation probably was even less at the time the current stand of small trees started than in 1947 and 1948 when the area was studied.

Data from this study do not indicate the critical densities of understory vegetation for establishment of either adequate or over-abundant pine reproduction. The data do indicate, however, that understory vegetation as dense as that on Meeks Table is definitely inhibitory to establishment of adequate ponderosa pine reproduction. The data from heavily grazed Devils Table support the theory that treatment which reduced the density of herbaceous understory vegetation has helped provide environments favorable to establishment of dense stands of advance tree reproduction. Reductions in density of virgin herbaceous understory vegetation provided better seedbeds for pine seed and resulted in less inter-specific competition to pine seedlings.

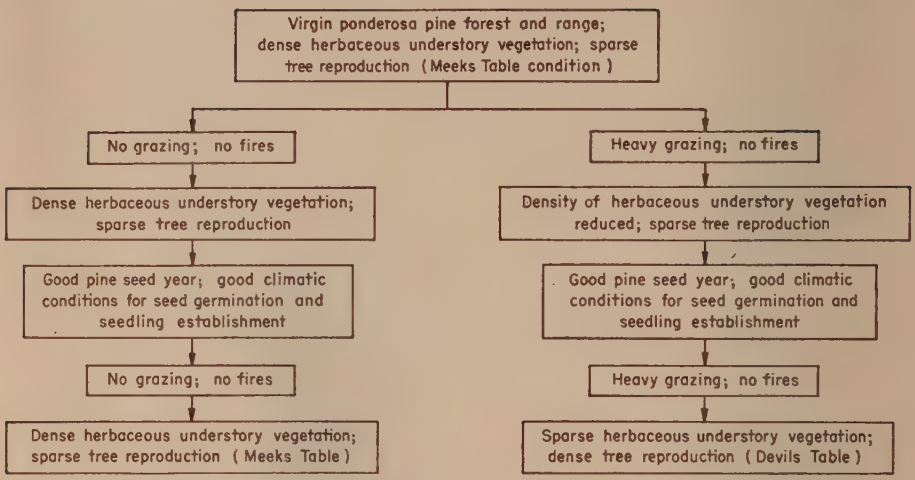
Virgin ponderosa pine forest and range; dense herbaceous understory vegetation; sparse tree reproduction (Meeks Table condition)
No grazing; no fires
Dense herbaceous understory vegetation; sparse tree reproduction
Good pine seed year; good climatic conditions for seed germination and seedling establishment
No grazing; no fires
Dense herbaceous understory vegetation; sparse tree reproduction (Meeks Table)
Heavy grazing; no fires
Density of herbaceous understory vegetation reduced; sparse tree reproduction
Good pine seed year; good climatic conditions for seed germination and seedling establishment
Heavy grazing; no fires
Sparse herbaceous understory vegetation; dense tree reproduction (Devils Table)

FIG. 8. Some sequential effects of livestock grazing and no livestock grazing, with absence of fire, on the virgin ponderosa pine forest and range, based on evidence from ungrazed Meeks Table and grazed Devils Table in central Washington.

Exclusion of fire may have contributed to the dense stands of advance ponderosa pine reproduction in some localities, but data from Meeks Table and Devils Table indicate that heavy livestock grazing must also be considered. Both areas had not been completely burned over for at least the past 125 years; yet Meeks Table supported only a handful of young trees, while Devils Table had 3,291 young trees per acre. As both areas had similar fire histories and were similar in all respects except livestock grazing, the large number of small trees on Devils Table appeared to have been fostered by heavy livestock grazing rather than fire.

The sequence of events leading to the present vegetation on Devils Table (Fig. 8) probably progressed this way: Livestock grazed down the heavy cover of range vegetation in the relatively open stands of virgin ponderosa pine. The reduction in ground cover made conditions favorable for establishment of seedling trees. A good seed-production year for pine coinciding with good climatic conditions, resulted in good catches of pine seedlings on the opened-up forest floor. The probable years in which many of the young trees on Devils Table started, 1903 and 1909, have been described as good seed years for pine; precipitation during 1903, 1904, and 1909 was generally above normal. Continued heavy grazing held the range vegetation at lowered densities and permitted the seedling trees to grow without severe grass competition. Livestock did little grazing damage to the growing trees and had little effect in thinning their numbers. During this recent period of 30 to 40 years, effective suppression of forest fires caused by lightning and man prevented any appreciable thinning out by fire. Similar sequences of events may have occurred on many other grazed ponderosa pine forest ranges in Washington and Oregon which now have stands of tree reproduction as dense or even denser than those found on Devils Table.

SUMMARY

A study of ungrazed Meeks Table and grazed Devils Table in central Washington provided evidence that parts of the virgin ponderosa pine (*Pinus ponderosa*) forest contained dense mats of herbaceous understory vegetation and sparse stands of tree reproduction. Pinegrass (*Calama-*

grostis rubescens) dominated and elk sedge (*Carex geyeri*) was a minor part of the understory virgin flora.

Densities of herbaceous understory vegetation on ungrazed Meeks Table were 183 per cent to 254 per cent of the densities on grazed Devils Table. Herbage yields of pinegrass were strikingly different between the two Tables. Pinegrass beneath open ponderosa pine produced 850 pounds of air-dry herbage per acre on Meeks Table compared to only 240 pounds on Devils Table. While the timber overstories on the two Tables were similar, Meeks Table had only a very few small trees but Devils Table had 3,291 small trees per acre.

The high density of herbaceous understory vegetation on Meeks Table contributed substantially to the deficiency of advance tree reproduction. Heavy grazing of the herbaceous understory vegetation, rather than exclusion of fire, appeared to be the prime factor in explaining the dense advance tree reproduction on Devils Table.

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A SMALL ISLAND COMMUNITY IN MIDSUMMER

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In many respects a small island is an ideal laboratory for ecologic investigations. The limited area and, usually, the smaller numbers of individuals and species, as compared with the mainland, make it easier to census the fauna and flora and to comprehend the interrelationships that exist. Furthermore, the peculiar insular situation, with fewer habitats available and often with the absence of competition typical of larger areas, brings about special responses on the part of island animals which help to point up the more involved relationships existing in larger communities. Little Rogg Island, situated in Potagannissing Bay at the eastern extremity of Chippewa County, Michigan, is such a spot near the upper end of Lake Huron. The present study was undertaken with a view to the population and distribution of small mammals, and most attention was centered thereon. Partial results have been published elsewhere (Manville 1950b). During a month's time (July 2 to 30, 1949) observations and specimens of many other members of the community were collected. These data are presented herewith as an indication of the island complex, although no clear-cut picture of the various interrelationships was obtained. The community is of further interest as representing a repopulation by the fauna and flora since a severe fire many years ago.

Acknowledgments

For permission to carry out this work on Little Rogg Island I am indebted to the late Hon. Chase S. Osborn and to Stellanova Osborn. Traps were supplied through the courtesy of Don W. Hayne. Aid in the identification of plants was kindly furnished by William B. Drew, Charles L. Gilly, and George W. Parmelee; and to the following individuals I am grateful for assistance in the determination of invertebrates: Irving J. Cantrall, Willis J. Gertsch, Clarence J. Goodnight, Justin W. Leonard, Walter F. Morofsky, Marion R. Smith, and Henry van der Schalie. A grant from the All-College Research Fund of Michigan State College was most helpful.

Description of Island

Northwest of Drummond Island and connecting the North Channel above with northern Lake Huron below, via Detour Passage, lies Potagannissing Bay, a beautiful and extensive body of water studded with islands of various sizes. Among the smaller of these is Little Rogg Island, having an area of some 9.5 acres. It is well sheltered from the prevailing westerly winds by Harbor and Boulanger Islands, each about one-half mile distant. To the east a channel about forty feet wide and five feet deep separates it from the larger Rogg Island (Fig. 1).

The principal axis of Little Rogg Island runs nearly north and south. The island is elongate in shape, quite narrow at the southern tip, and measures 1,300 feet in length by 500 feet in greatest width. The terrain is generally smooth, being steeper along the eastern shore, and the maximum elevation is some twenty feet above the waters of the bay.

Except for a narrow fringe of beach the island is today well forested. The beach consists mostly of stones and gravel, but at the northern and southeastern portions are small sandy shores. The beach is widest along the southern and western margins, reaching about twenty feet in extent; along the eastern margin only a few feet of beach separate the water and the overhanging trees, and here much of the forest is rooted in a terrace of rocks some six feet high. The whole island,

FIG. 1. View northward across the channel between Rogg Island, at the right, and Little Rogg Island; Harbor Island appears in the distance. July 13, 1949.

for that matter, is underlain by rocks, but a good layer of earth and duff covers most of the forested portion.

During the month of July, 1949, the temperature on nearby Drummond Island ranged from 46° to 90° F. The mean minimum temperature was 59.2°, the mean maximum 77.5°, and the monthly mean 68.4°. There were fourteen clear days, fourteen partly cloudy, and three cloudy; rain fell on ten different days. No further meteorological data are available for the near vicinity, but the following summary of conditions for forty years at Sault Ste. Marie, some forty miles to the northwest, taken from Wills (1941), will give an idea of the climate of the area: average January temperature, 14.2° F.; average July temperature, 64.1°; maximum temperature, 98°; minimum temperature, — 37°; last killing frost in spring, May 14; first killing frost in fall, October 3; length of growing season, 142 days; average annual precipitation, 28.85 inches. The waters surrounding the island are, of course, completely frozen over during the winter.

Little Rogg Island is seldom disturbed by man. Potagannissing Bay is a mecca for fishermen, but few visit the island except for shelter, during occasional thunderstorms. Some hunters invade it in the autumn, in quest of deer which frequent many of the islands in the bay. There are no buildings or man-made structures on the island. There is ample evidence of a severe fire which swept across the island many years ago; local informants place the year at about 1910. The forest was apparently rather completely destroyed, and presumably the animal life as well. Today Little Rogg Island is again well forested. This conflagration did not affect Rogg Island to the east.

VEGETATION

The predominant trees of the island are white cedar, aspen, and balsam fir, with white spruce and white birch interspersed. There are a few scattered mountain ash, pin cherry, and white ash. Near the shores tag alder is common, with an occasional tamarack or clump of red-osier dogwood. The forest floor is well covered by a variety of herbaceous plants and shrubs, and frequent scorched remains of old trees (Fig. 2). In a central area, covering about a quarter of the island, bracken and patches of grass are the chief ground cover, and aspen and white birch the principal trees. Sugar maples are

represented only by scattered seedlings over the island. Along the shores are areas of reeds and sedges, and here are found the few examples of horsetail, iris, smartweed, silverweed, beach pea, jewelweed, and horehound. I observed no *Lycopodium* anywhere on Little Rogg Island. The vegetation of Rogg Island to the east is quite similar but further developed, with many mature sugar maples and extensive clumps of thimbleberry (*Rubus parviflorus* Nutt.) and red raspberry (*Rubus idaeus* Linn.).

No quantitative data on the vegetation were secured, nor were attempts made to collect all the plant species present. The more common or conspicuous elements of the flora are listed below; in addition, a variety of unidentified fungi and mosses was present.

Herbaceous plants on Little Rogg Island included the following: *Pteridium aquilinum* (L.) Kuhn, *Botrychium virginianum* (L.) Sw., *Equisetum arvense* L., *Sparganium eurycarpum* Engelm., *Agrostis scabra* Willd., *Calamagrostis inexpansa* Gray, *Phalaris arundinacea* L., *Phragmites communis* Trin., *Carex hystericina* Muhl., *Carex striata* Lam., *Lilium philadelphicum* L., *Maianthemum canadense* Desf., *Streptopus amplexifolius* (L.) DC, *Iris versicolor* L., *Habenaria hookeri* Torrey, *Corallorrhiza striata* Lindl., *Urtica gracilis* Ait., *Polygonum punctatum* Ell., *Polygonum convolvulus* L., *Phytolacca decandra* L., *Anemone canadensis* L., *Anemone cylindrica* Gray, *Ranunculus acris* L., *Sisymbrium altissimum* L., *Mitella nuda* L., *Potentilla anserina* L., *Lathyrus maritimus* (L.) Bigel., *Trifolium hybridum* L., *Trifolium repens* L., *Impatiens biflora* Walt., *Hypericum kalmianum* L., *Hypericum perforatum* L., *Aralia nudicaulis* L., *Pyrola elliptica* Nutt., *Monotropa uniflora* L., *Trientalis americana* (Pers.) Pursh., *Asclepias incarnata* L., *Verbena hastata* L., *Lycopus americanus* Muhl., *Prunella vulgaris* L., *Satureja vulgaris* (L.) Fritsch, *Verbascum thapsus* L., *Galium triflorum* Michx., *Linnaea borealis* L., *Lobelia kalmii* L., *Eupatorium perfoliatum* L., *Solidago juncea* Ait., *Erigeron pulchellus* Michx., *Anaphalis margaritacea* (L.) B & H, *Achillea millifolium* L., *Chrysanthemum leucanthemum* L., *Cirsium arvense* (L.) Scop, *Cirsium vulgare* (Savi) Airy-Shaw, *Taraxacum officinale*

FIG. 2. View of a typical forest area on the southern half of Little Rogg Island. July 14, 1949.

Weber, and *Hieracium canadense* Michx.

Trees and shrubs present were as follows: *Larix laricina* (Du Roi) Koch, *Picea canadensis* (Mill.) BSP, *Abies balsamea* (L.) Mill., *Thuja occidentalis* L., *Juniperus canadensis* Burgsd., *Populus tremuloides* Michx., *Betula alba* L., *Alnus incana* (L.) Moench., *Ribes setosa* (Lindl.) Cav. & Britt, *Pyrus americana* (Marsh.) DC, *Prunus pennsylvanica* L., *Acer saccharum* Marsh., *Shepherdia canadensis* (L.) Nutt., *Cornus stolonifera* Michx., *Vaccinium* sp., and *Fraxinus americana* L.

Invertebrates

The invertebrates collected certainly represent only a portion of those present on the island, but their enumeration below gives an idea of the diversity of types. Included in the list are both terrestrial and aquatic free-living forms, each of which contributes to the ecologic complex of Little Rogg Island. No earthworms were observed on the island, despite frequent searching for them; they were present on Drummond Island. There was a notable variety of spiders, including one form, *Tetragnatha* sp., as yet undescribed. On July 2 the exuviae of literally millions of mayflies were washed up in windrows on the shore. Among the other insects, the variety of beetles and of ants was of interest. The dipterans, of course, included many famous northern biters, such as the horse fly, deer fly, stable fly, midges, and mosquitoes. Parasitic forms were noted only on the mammals collected.

Among the invertebrates present on Little Rogg Island, the only annelid noted was the leech, *Haemopis marmoratis* Say. Crustaceans included the sow bug, *Cylisticus convexus* De Geer, and the crayfish, *Cambarus virilis* Hagen. Arachnoids were represented by the phalangid, *Leiobunum calcar* Wood, and by the following spiders: *Amaurobius bennetti* Blackwall, *Agelenopsis utahanus* Chamberlin & Ivie, *Neoantistea radula* Emerton, *Dolomedes tenebrosus* Hentz, *Pardosa lapidicina* Emerton, *Theridion tepidariorum* Koch, *Aranea displicata* Hentz, *Aranea trifolium* Hentz, *Neoscona arabesca* Walckenaer, *Tetragnatha versicolor* Walckenaer, *Tetragnatha laboriosa* Hentz, *Philodromus aureolus* Clerck, *Misumena vatia* Clerck, and *Herpyllus vasifer* Walckenaer. The only myriapod was a species of *Leptodesmus*.

Insects included the following forms: Orthoptera—*Chloealtis conspersa* Harris, *Camnula pellucida* Scudder, *Dissosteira carolina* Linn., *Melanoplus bivittatus* Say, *Melanoplus huroni* Blatchley, and *Gryllulus assimilis* Fabr.; Ephemeroptera—*Hexagenia limbata* Guerin; Odonata—*Boyeria vinosa* Say, *Basiaeschna janata* Say, *Macromia illinoisensis* Walsh, *Sympetrum rubicundulum* Say, *Ischnura verticalis* Say, and *Enallagma carunculatum* Morse; Hemiptera—*Apaticus cynicus* Say; Homoptera—*Tibicen linnei* Smith & Grossbeck, *Ceresa dorsalis* Walker, and *Philaenus leucophthalmus* Linn.; Coleoptera—*Silpha americana* Linn., *Ludius medianus* Germ., *Melanotus fissilis* Say, *Dicera tuberculata* Cast., *Bupresta maculativentris* Say, *Phyllophaga* sp., *Xylaryetes satyrus* Fabr., *Ceruchus piceus* Web., *Bolitothermes cornutus* Panz., *Upis ceramboides* Linn., *Tenebrio molitor* Linn., *Brachyrhinus ovatus* Linn., *Chilcorus* sp., *Carabus serratus* Say, *Poecilus* sp., *Patrobus longicornis* Say, *Bembidion* sp., and *Pterostichus* sp.; Lepidoptera—*Malacosoma americana* Fabr., *Papilio turnus* Linn., *Argynnis cybele* Fabr., *Vanessa antiopa* Linn., *Basilarchis arthemis* Drury, and *Danais archippus* Fabr.; Diptera—*Culicoides* sp., undetermined mosquitoes, *Tabanus atratus* Fabr., *Tabanus trispilus* Wied., *Chrysops vittata* Wied., *Chrysops celer* O.S., *Asilus* sp., *Eristalis transversus* Wied., *Zenillia* sp., *Musca domestica* Linn., and *Stomoxys calcitrans* Linn.; Hymenoptera—*Bombus vagans* Fabr., *Vespa communis* Sauss., *Thyreodon morio* Fabr., *Tapinoma sessile* Say, *Camponotus herculeanus* var. *whymperi* Forel, *Camponotus herculeanus liquiperdus* var. *noveboracensis* Fitch, *Formica sanguinea*

subnuda Emery, *Formica sanguinea aserva* Forel, and *Formica fusca* Linn.

The molluscs present were as follows: Gastropods—*Lymnaea catascopium* Say, *Lymnaea stagnalis appressa* Say, *Helisoma campanulatum* Say, *Physa ancillaria* Say, *Mesodon zaletus* Binney, *Deroceras laeve* Müller, *Anguispira alternata* Say, *Campeloma integrum* Say, and *Goniobasis livescens* Menke; Pelecypods—*Lampsilis siliquoidea rosacea* De Kay and *Sphaerium* sp.

Amphibians and Reptiles

Only the green frog, *Rana clamitans* Latreille, and the garter snake, *Thamnophis sirtalis* Linnaeus, were observed on Little Rogg Island, but possibly other species were present, although certainly not conspicuous. On adjacent Rogg Island only the green frog was observed, and the snakes included the red-bellied snake, *Storeria occipitomaculata* Storer, as well as the garter snake. In contrast to these specimens from the small islands in the bay, the following species in addition to those already mentioned were noted on Drummond Island: the American toad, *Bufo americanus* Holbrook; the common tree-toad, *Hyla versicolor* Le Conte; the leopard frog, *Rana pipiens* Schreber; the wood frog, *Rana sylvatica* Le Conte; the green snake, *Opheodrys vernalis* Harlan; the water snake, *Natrix sipedon* Linnaeus; and the painted turtle, *Chrysemys bellii* Gray.

Birds

Although twenty-five species of birds were noted on Little Rogg Island, many of these were thought to be visitors from Rogg Island or more distant points. Those observed on Little Rogg Island during July were the following: lesser loon, *Gavia immer elasson* Bishop; great blue heron, *Ardea herodias* Linnaeus; lesser scaup duck, *Aythya affinis* Eyton; American merganser, *Mergus merganser americanus* Cassin; eastern red-tailed hawk, *Buteo jamaicensis borealis* Gmelin; osprey, *Pandion haliaetus carolinensis* Gmelin; killdeer, *Charadrius vociferus* Linnaeus; spotted sandpiper, *Actitis macularia* Linnaeus; herring gull, *Larus argentatus smithsonianus* Coues; common tern, *Sterna hirundo* Linnaeus; black-billed cuckoo, *Coccyzus erythrophthalmus* Wilson; belted kingfisher, *Megaceryle alcyon* Linnaeus; flicker, *Colaptes auratus* Linnaeus; hairy woodpecker, *Dryobates villosus* Linnaeus; downy woodpecker, *Dryobates pubescens* Linnaeus; olive-sided flycatcher, *Nuttallornis borealis cooperi* Nuttall; tree swallow, *Iridoprocne bicolor* Vieillot; eastern crow, *Corvus corone brachyrhynchos* Brehm; black-capped chickadee, *Penthestes atricapillus* Linnaeus; eastern robin, *Turdus migratorius* Linnaeus; myrtle warbler, *Dendroica coronata* Linnaeus; black-throated green warbler, *Dendroica virens* Gmelin; Blackburnian warbler, *Dendroica fusca* Müller; fox sparrow, *Passerella iliaca* Merrem; and song sparrow, *Melospiza melodia* Wilson.

My limited observations indicated that there were eighteen pairs of breeding birds, or at least eighteen occupied territories, of ten species on Little Rogg Island. Actual nests were located only in five cases. Locations where birds were repeatedly seen, especially in the case of singing males, were recorded. In several other cases young were seen, out of the nests, or adults were observed feeding young. From these data I have constructed a rough map of the distribution of the territories (Fig. 3). A black spot indicates an actual nest site; the closed lines suggest the territorial limitations of the various pairs or singing males. Song sparrows (4 pairs) and black-throated green warblers (3 pairs) were the most numerous breeding birds.

From this it appears that there were 1.8 territories or pairs per acre on Little Rogg Island during this month. This figure is nearly the same as that found by Kendeigh (1948) in a 33-acre cedar-aspen community in northern lower Michigan; it is somewhat lower than that

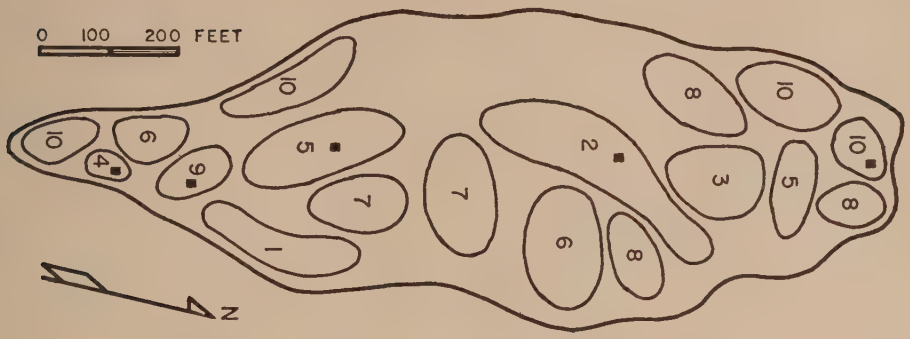

FIG. 3. The approximate distribution of breeding bird territories on Little Rogg Island during July, 1949. *1,* black-billed cuckoo; *2,* flicker; *3,* hairy woodpecker; *4,* tree swallow; *5,* black-capped chickadee; *6,* robin; *7,* myrtle warbler; *8,* black-throated green warbler; *9,* Blackburnian warbler; *10,* song sparrow. Dots represent nest locations.

reported by Cruickshank and Cadbury (1950) for a 30-acre tract of red and white spruce on Hog Island, Muscongus Bay, Maine.

In addition to these resident birds, kingfishers were frequently seen along the eastern side of the island, but it was thought they bred across the channel on Rogg Island. The apparently unoccupied space at the western side of the island is difficult to account for; the habitat here appeared similar to that elsewhere. It was near here that one fox sparrow, perched on a small tamarack, was observed in full song on July 4; it was not seen or heard again, however. On several occasions an immature red-tailed hawk was seen perched on a dead tree top near the center of the island.

On Drummond Island, fifty-five species of birds were noted at odd times during the month; doubtless many others were present, and most of these were probably breeding forms. It is quite possible that some of these occasionally visit Little Rogg Island; but it is not surprising, in view of the size and the relatively uniform habitat of the island, that more birds did not breed there.

MAMMALS

On Little Rogg Island I found evidence of only eight different kinds of mammals. This was rather surprising in view of the twenty-three species known to occur today on Drummond Island (Manville 1950a). Perhaps the severe fire some years ago and the relatively small size and isolated nature of the island have combined to keep the mammal population down.

White-tailed deer, *Odocoileus virginianus borealis* Miller, were present on Little Rogg Island at the beginning of my study. Tracks of an adult and a fawn were common nearly everywhere, and a doe was seen at the north end of the island on July 7. On July 8 a doe and spotted fawn together were seen across the channel on Rogg Island, and subsequently elsewhere. They did not again appear on Little Rogg. The skeleton of a fawn found near the beach on Little Rogg was considered a hunting fatality from some previous season.

No snowshoe hares, *Lepus americanus* Erxleben, were seen on Little Rogg Island, but some old scats were noted. Possibly the hares vacated the island over the ice during the previous winter. Red squirrels, *Tamiasciurus hudsonicus* Erxleben, were often seen and heard, and middens of spruce cones were frequent. Two subadult females were collected; both were infested with fleas. It is felt that the island population of red squirrels at this time consisted of one adult pair and their young of the year. Both hares

and red squirrels were present on Rogg Island.

Several aquatic mammals visited the island occasionally. Tracks and sign of mink, *Mustela vison* Schreber, were noted on the eastern and northern shores. Muskrats, *Ondatra zibethica* Linnaeus, were evidenced by bank burrows and gnawings on reeds along the southeastern shore. No recent signs of beaver, *Castor canadensis* Kuhl, were noted, but an old aspen stump four inches in diameter, at the northern end of the island, attested to their former presence.

Most of my efforts were directed toward the remaining two mammals of Little Rogg Island: the woodland deer mouse, *Peromyscus maniculatus gracilis* Le Conte, and the meadow vole, *Microtus p. pennsylvanicus* Ord. Both these species occurred also on Rogg Island, as did the red-backed vole, *Clethrionomys g. gapperi* Vigors. Attempts to secure the latter on Little Rogg Island were fruitless.

My technique of marking and releasing animals captured in live traps set in checkerboard pattern over the entire island is described more fully elsewhere (Manville 1950b). Trapping was in progress continuously from July 3 to 30, with a total of 1,698 trap-nights. Until the last three days live traps were employed, with over half the *Microtus* population dying in the traps; the remainder were removed with snap traps during the final three days. It is felt that all resident small mammals on the island were captured during this time, except possibly for some juveniles not yet out of the nests.

Apparently the entire island population of deer mice consisted of two females. Both were adults, and neither showed evidence of having bred. This disheartening situation seems to suggest that these two mice were comparatively recent arrivals on the island, perhaps carried thence with driftwood or coming across from Rogg Island on the ice. One was taken at three different locations on the southern quarter of the island, the last capture being on July 7; the other was taken but once at the center of the island, on July 10. Both were apparently healthy when released, but neither was taken again. Both were parasitized by fleas.

Scarcely less surprising than the absence of red-backed voles and the paucity of deer mice was the predominance of meadow voles, especially as the island contained no meadows and very few small patches of sparse grass. The situation was somewhat similar to that described by Dice (1925) on Marion Island, where voles overran all types of forest habitat. Here the voles lived among conifers, deciduous trees, bracken and other ground cover, and several were even taken among the loose pebbles and rocks composing the eastern shore of the island.

There were twenty-five adult and subadult meadow voles on Little Rogg Island; of these, twelve were males and thirteen females. In addition, one juvenile female was captured on July 30, apparently venturing out of the nest for the first time. Of the twelve males, seven were adults and five subadults; of the thirteen females, six were adults and seven subadults. Thus the concentration of adult and subadult voles on the island approximated 2.6 per acre at this time.

Two of the adult females showed no external evidence of breeding; they were captured between July 10 and 17. The other four were all in breeding condition. One was lactating (July 17); one contained five embryos, average length 20 mm. C.R. (July 8); one contained four embryos, average length 16 mm. C.R. (July 28); and one contained three embryos, all in the right horn of the uterus, average length 10 mm. C.R. (July 28). Of the seven adult males, only one showed no evidence of breeding (July 10); in all the others the testes were enlarged, and usually scrotal in position, between July 7 and 26. Most of the subadults came into breeding condition during the month. In five of the subadult females, evidence of breeding was noted as early

as July 17; one contained five embryos, average length 5 mm. C.R. (July 28); and one was lactating on July 29. In three of the subadult males, the testes were descending by July 18, and in two they were scrotal in position by July 29.

The home ranges, based on points of capture, were computed as I have done formerly (Manville 1949) for individuals captured three or more times. The home ranges of adult voles appeared to be rather well defined. In the case of five adult females (Fig. 4) they ranged from 1,000 to 1,800 square yards, and averaged 1,320 square yards. The home ranges of three adult males (Fig. 4) ranged from 2,000 to 2,400 square yards, and averaged 2,266 square yards. As regards all thirteen adults, captures ranged from one to five per individual, and averaged three. The home ranges of subadults were apparently less well defined. They fell into no such pattern as did those of the adults, for these younger individuals seemed to be still seeking home areas to establish for themselves. The greatest recorded movement of any individual was that of a subadult female taken at points 960 feet apart (A and B, Fig. 4) at 10:00 and 10:30 A.M., respectively, on July 22.

The map (Fig. 4) indicates that the adult voles remain within restricted home ranges. This is more pronounced in females, where in none of the five cases was there any overlapping in the home ranges as approximately from points of capture. This was also the case with the three adult males illustrated, but there were two cases among adult males captured less than three times where two individuals were captured in the same trap, although on different occasions. Younger individuals, not having yet established their home areas, exhibited no such behavior. There was considerable overlapping in the distribution of subadults with individuals of other sex- and age-groups.

External parasitism was evident in all but four of the twenty-six voles captured; these four were dead at the initial capture, and the parasites may have deserted them before examination was possible. Nine were parasitized by fleas; fifteen by red mites, in each case apparent only on the pinnae; two by lice; and three by seed ticks on the neck or face. There appeared to be no correlation between presence of these parasites and either age or sex of the host.

Only two individuals showed any indication of intraspecific strife or attack by predators. One adult male lacked the tip of the tail, the stump being well healed; and one subadult female had the left ear badly torn, as though by fighting. This slight evidence of fighting is not surprising, with the population so low that competition should have been negligible. In

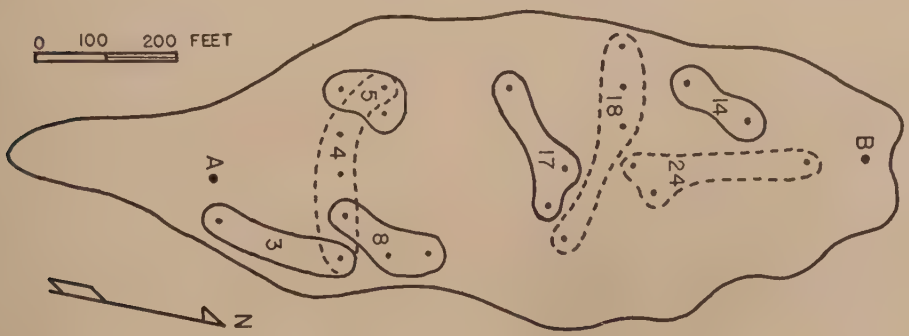

FIG. 4. The apparent home ranges of eight adult *Microtus* captured three or more times. Numbers are those of marked individuals; solid lines indicate females, broken lines males; each dot represents the location of one trap where caught. *A* and *B* indicate successive points of capture of a subadult female *Microtus* at half-hour intervals on July 22.

contrast, there were two instances of apparent sociability among the voles, as indicated by multiple captures in the traps designed to take one animal at a time. In one case, an adult male and an adult female were captured together; in the other case, an adult male and a subadult male occupied the same trap.

Discussion

A cursory study of this sort can scarcely uncover any deep-lying ecologic principles. And yet it was evident that on this small island were manifest such fundamental relationships as those between predator and prey, host and parasite, and those exemplified in the pyramid of numbers. One principle seemingly illustrated by *Microtus* was the atypical habitat selection in this island community; in the absence of competition from other closely related species, the voles were less selective as to habitat and spread out into types of cover not usually associated with them on mainland areas. A small island such as this would appear to be an ideal situation for many sorts of ecologic studies.

Of particular interest in the case of Little Rogg Island was the question of the source of the fauna, for it seems probable that the island was depopulated by a severe fire about 1910. The various factors of distribution operating on such islands as this have been well outlined by Hatt *et al.* (1948). Aside from the spiders, sow bugs, harvestmen, and land snails, nearly all the invertebrates on Little Rogg Island are either aquatic or aerial in some stage of their existence. Transportation by the wind would seem to account for the arrival of spiders, and the few other cases can probably be charged to dispersal by some fortuitous circumstance, such as drifting in flotsam or attached to other animals.

The vertebrates, aside from the birds and the aquatic members, are a somewhat different case. The garter snake, although primarily terrestrial, is well known for its penchant for swimming; and Rogg Island is a convenient source for repopulation. Several of the mammals on Little Rogg Island are capable swimmers, and pose no problem. The others (snowshoe hare, red squirrel, deer mouse, and meadow vole) are active throughout the winter, and could easily cross to the island on the ice. This is almost too obvious to mention in the case of the hare and squirrel. The two smaller rodents may not travel so widely, but even so Rogg Island is near enough to be a ready source. I believe it is only a matter of time until red-backed voles, and possibly shrews and other mammals, will also arrive and become established on Little Rogg Island.

Summary

During July, 1949, studies were made on a 9.5-acre island near the northern tip of Lake Huron. The island is well forested, chiefly with conifers and aspen. A severe fire about 1910 presumably destroyed the fauna and flora; the life present on the island today gives an interesting picture of the repopulation of such a small isolated habitat.

Listed are 55 species of herbaceous plants and 16 trees and shrubs now present on the island. The most conspicuous animal life included 15 spiders, 59 insects of nine orders, 9 gastropod molluscs, and 7 other invertebrates; one amphibian, one reptile, 25 birds, and 8 mammals comprised the vertebrates of the island. The apparent absence of *Lycopodium* and of earthworms was noteworthy.

Eighteen pairs of breeding birds occurred on the island; their apparent distribution is figured. This represented a concentration of 1.8 territories per acre during this time.

Most attention was focussed on the small mammal population, which was dominated by the meadow vole, *Microtus pennsylvanicus*. This situation was surprising not only because of the unusual habitat for this species, but also because

the entire adult and subadult population consisted of only 25 individuals—a concentration of 2.6 per acre, as determined by extensive live-trapping. The apparent home ranges of eight adult males and females are presented graphically, and suggest that these voles tend to stay within restricted home ranges, larger in the case of males. Breeding behavior, external parasites, and general habits of the voles are discussed briefly.

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AN ANALYSIS OF THE PLANT COMMUNITIES OF MARY'S PEAK, WESTERN OREGON [1]

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INTRODUCTION

Data were obtained on Mary's Peak in the Coast Range of western Oregon during the summer of 1947 to test the application of the several phytosociological concepts concerned in the analysis and description of plant communities. These concepts are based largely on quantitative and qualitative characteristics. The quantitative characteristics studied are abundance, coverage, and frequency; for trees, basal area and size classes computed from field measurements of diameter at breast height (DBH) were also considered. Qualitative characteristics studied include sociability, vitality, periodicity, stratification, and life forms (Braun-Blanquet 1932, Cain 1932, Lutz 1930). Although the results and conclusions may be tested for these samples of vegetation, no final conclusions can be made until many more such studies are made in similar and different types of communities and a comparison made.

LOCATION, PHYSIOGRAPHY, AND TOPOGRAPHY

Mary's Peak, rising to an elevation of 4,097 feet, is the highest point of the Oregon Coast Range north of the Umpqua River (Fig. 1). It is a large mass of fine grained diorite intruded into Eocene sedimentary rocks (Washburne 1914). The mountain is located near the western edge of Benton County in western Oregon about 26 miles from the Pacific Ocean. It is about 44° 30′ north latitude and 123° 33′ west longitude in T12S R7W of the Willamette Meridian and is included in the Mary's Peak and Alsea quadrangles as surveyed by the Corps of Engineers, U.S. Army. It is 15 miles southwest of Corvallis and can be reached by State Highway 34 which branches from U.S. Highway 20 at Philomath, Oregon.

The Oregon Coast Range Mountains between the Olympic Mountains on the north and the Klamath Mountains on the south are all included in the Pacific Border province (Fenneman 1931). The general aspect of this range is that of a dissected plateau or upraised peneplain. The elevations of the crests range from about 1,700 feet in northern Oregon to about 3,000–3,500 feet near the Klamath Mountains.

The sedimentary rocks are of Cenozoic age and generally weak. The volcanic rocks are contemporaneous or intruded into the sediments. These intrusives form the highest peaks, including Mary's Peak, Saddle Mountain in Clatsop county, and several others.

The drainage pattern of the Mary's Peak area is radial. The north and east slopes drain into the Willamette River at Corvallis. The south and west slopes drain into streams that empty into the Pacific Ocean to the west (USDA Forest Service 1937).

The topography of Mary's Peak includes some very steep slopes below the summit and the ridges. The contour lines indicate a slope of 1,000 to 1,250 feet vertically in a distance of 3,000 feet horizontally, or a 33 per cent to approx-

[1] The author wishes to acknowledge his appreciation to the following members of the staff of Oregon State College who have helped in various phases of the work: To my major professor, Dr. Henry P. Hansen, for his suggestions and criticisms, to Dr. Helen M. Gilkey, for help in the identification of several difficult plant specimens, and to Drs. E. L. Packard and I. S. Allison, for help in the geological description of the area. I am grateful also to my wife, Cherrie, for encouragement and assistance.

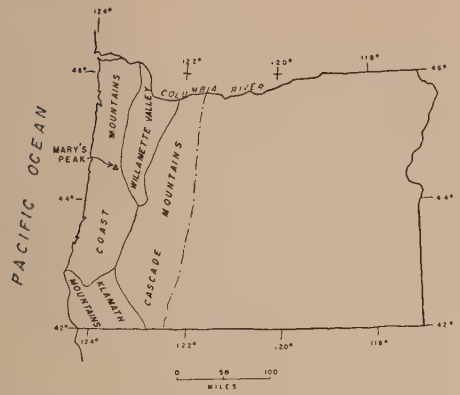


FIG. 1. Map showing the physiographic provinces of western Oregon and the location of Mary's Peak.

imately 40 per cent slope. Some places, on the south side of the mountain, have a drop of 1,000 feet in 2,000 feet for a 50 per cent slope.

CLIMATE

The Coast Range of Oregon has a wet, microthermal climate with adequate precipitation at all seasons according to Thornthwaite's (1931) classification of North American climates. The climate is typically marine due to the proximity of the Pacific Ocean and the prevailing westerly winds.

The narrow belt west of the Coast Range has a very equable climate. In this belt there is little freezing weather, and on the rare occasions when snow falls, it seldom remains on the ground more than a few hours. The normal annual temperature ranges from about 50° to 52° F. The rainfall in this belt ranges from 50 to more than 100 inches, depending on the height of the Coast Range and the nearness of the hills to the ocean. Precipitation occurs mostly as gentle rain, and sudden downpours are rare. The winds off the ocean are persistent but seldom reach destructive force.

The Coast Range has a more varied climate. In general, the normal annual temperature is below 50° F. There is considerable freezing weather in winter, and in places the snow becomes quite deep at times. The normal annual precipitation ranges from about 50 inches to more than 130 inches. Most of this region is heavily forested, but farms have been established in many valleys where the forest has been removed.

The Willamette Valley, lying between the Coast and Cascade Ranges in Oregon, has an equable climate, though ranges in temperature are greater than those of the coast. The normal annual temperature is mostly between 51° and 53° F. Some freezing weather occurs every winter, and most stations have had minima of zero or somewhat lower. The average growing season is a frostless period of about 200 days. The normal annual precipitation in the Corvallis area is about 39 inches. Most of the precipitation occurs as gentle rain, but there is some showery weather in spring and summer, and an average of about 6 inches of snow in the winter. There is a pronounced dry season in summer (U.S. Weather Bureau 1930). In summary, precipitation is decidedly seasonal in character. West of the Cascade Mountains 44 per cent of the precipitation occurs in winter, 24 in spring, 5 in summer, and 27 in autumn (USDA Weather Bureau 1947). At the higher elevations, as on Mary's Peak, the growing seasons are somewhat shorter as snow falls above approximately 2,500 feet soon after the middle of October and disappears approximately late March or early April except for a few pockets on steep north and east slopes. The prevailing winds are westerly and attain high velocity near the summit of the mountain.

GENERAL VEGETATION DESCRIPTION

Mary's Peak lies within the cedar-hemlock association of the coast forest (Weaver and Clements 1938). Neither of these species, however, is very abundant in this area, especially below 2,500 feet elevation. The principal forest species of the Coast Range is *Pseudotsuga*

taxifolia[2] (Douglas fir). In the cedar-hemlock climax of the Puget Sound region and the southern part of the Olympic Peninsula, *Pseudotsuga taxifolia* is a subclimax species that has persisted as a result of fires that must have occurred periodically throughout postglacial time. In the Coast Range of Oregon, however, the climate at lower elevations is apparently too dry for *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) to thrive sufficiently well to attain climax status. *Pseudotsuga taxifolia* maintains a climax status in this area and fire is not necessary in order for it to persist here (Munger 1940). The relative dearth of hemlock during the entire postglacial time is indicated by the low proportions of its pollen in peat sections in the Willamette Valley (Hansen 1947). Other species in the Coast Range locally abundant where conditions are favorable, are *Abies procera* (noble fir) on some of the higher peaks, *Abies grandis* (lowland white fir) broadly distributed and with local abundance, *Abies amabilis* (silver fir) at isolated stations in the northern part of the Coast Range of Oregon and becoming more abundant northward into Washington, *Pinus monticola* (western white pine) at higher altitudes but rare, and *Quercus garryana* (Oregon white oak) at lower altitudes on the eastern slope of the Coast Range and into the Willamette Valley to the east.

Hemlock-noble fir-Douglas fir community

The north slope of Mary's Peak above 2,500 feet elevation (Fig. 2) is covered predominantly by *Tsuga heterophylla* ranging from seedling and small tree size to about 24 inches DBH and 80 or more feet tall. *Abies procera* is most common above 3,400 feet elevation and ranges in size from seedlings to specimens 48 inches DBH and 150 or more feet tall. An almost pure stand of this species occurs just below the summit at 3,600–3,800 feet. Below 3,400 feet it becomes more scattered and below 2,500 feet it is very sparse. *Thuja plicata* occurs mostly as small trees less than 10 inches DBH on moister sites about springs and along the streams. *Pseudotsuga taxifolia* is represented by scattered giant specimens 44–60 inches DBH and 150 or more feet tall. Seedlings on the forest below 3,600 feet elevation consist largely of *Tsuga heterophylla.* Other seedlings are those of *Abies procera* and *Pseudotsuga taxifolia.* According to Munger (1940: 454), *Pseudotsuga taxifolia* seeds germinate on the forest floor, but the seedlings, in contrast to those of *Tsuga heterophylla,* do not survive in the shade. In the area of *Tsuga heterophylla* or *Abies procera* predominance, there is no understory of young *Pseudotsuga* trees. The latter is a shade intolerant aggressive tree that forms pure even-aged stands after fire or logging and is gradually replaced by shade tolerant trees where moisture conditions are favorable for their survival. This successional cycle does not occur generally in the southern part of the Douglas fir region, which is less favorable for *Tsuga, Thuja,* and *Abies* (Munger 1940), but does take place on the north slope of Mary's Peak. On the south and east slopes the cycle is not noted, especially below 3,400 feet, except in ravines or valleys, and here *Pseudotsuga* is apparently climax. This is the pioneer large tree species as well as the climax. Young trees are found only in openings, never under the canopy of the forest whether it consists of *Pseudotsuga* alone or any of the other tree species. Fig. 2 shows two small areas of hemlock with Douglas fir on the south slope. The area between the two burns is along a small stream. Connor's Camp is in a valley between Mary's Peak and a ridge to the south.

The south and west slopes of mountains farther inland are generally drier than north and east slopes because of more direct and longer exposure to the sun.

[2] The nomenclature follows that of Peck (1941), Gilkey (1946), and Hitchcock (1935).

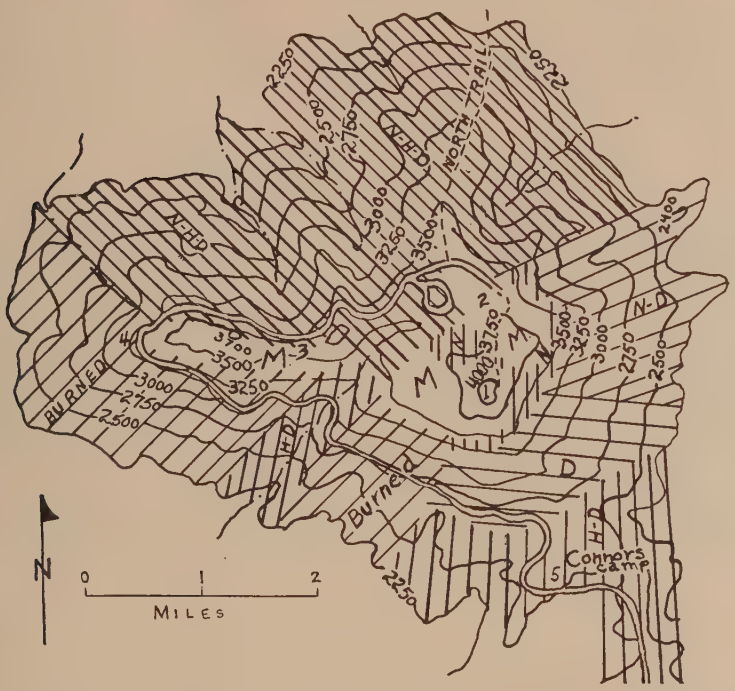


FIG. 2. Map of Mary's Peak above the 2,500 foot contour showing the plant communities. Abbreviations refer to the following plant communities: N—noble fir, D—Douglas fir, ND—noble fir-Douglas fir, NHD—hemlock-noble fir-Douglas fir, HD—hemlock-Douglas fir, M—meadow, B—a recently burned area. The numbers refer to locations mentioned in the text: 1—summit, 2—present parking area, 3—old parking area, 4—the "Big Curve" in the road at the west side, 5—Connor's Camp area. (U.S. Army Engineers, Mary's Peak Quadrangle 1942.)

However, the situation in the Coast Range is somewhat different. The south and north slopes differ as above, but the west slopes are windward to the moisture laden prevailing westerly winds from the Pacific Ocean, and the east slopes are leeward. Thus, the west slopes are moister and above 1,000 feet support a relatively abundant stand of *Tsuga,* whereas the drier east and south slopes support *Pseudotsuga* as a climax tree (Munger 1940).

At about 2,500 feet elevation on the north slope of Mary's Peak is the upper limit of a burn that occurred about 1908. The forest here is composed of a dense growth of young *Pseudotsuga* that is about 30 years old and 4–12 inches DBH. The living trees, snags, and fallen dead trees form a tangled mass that can be penetrated only with great difficulty. *Tsuga* has begun to invade this area, but only on the upper part.

The herbaceous layer of the north slope is composed largely of *Oxalis oregana* (wood sorrel), which often forms a green "carpet" except where *Tsuga* is predominant. The ground is practically devoid of vegetation under the *Tsuga* and the litter may be 1–3 inches deep in the more level areas. This condition is also described by Stearns (1951) for patches of *Tsuga canadensis* (L.) Carr. in Wisconsin. *Gaultheria shallon* (salal) and *Berberis nervosa* (Oregon grape) are almost entirely absent on this slope.

FIG. 3. View eastward across the meadow from near the west end toward the summit (El. 4097 ft.). The trees at left are the upper part of the hemlock-noble fir-Douglas fir community on the north slope. The trees (hemlock-Douglas fir) in the middle distance bisect the meadow along a small ravine. The trees on the right are noble fir and the upper limits of Douglas fir on the south slope. The prevailing winds are from right to left. One line of quadrats extended from foreground in center of picture to the tower on the summit. Sign at lower left is at 3 on map. (Oct. 1947.)

Various grasses, as *Trisetum cernuum* and *Bromus vulgaris,* are found in small open spaces, and also certain forbs, especially *Senecio triangularis* (ragwort). The most common shrub in open areas and along edges of timber is *Holodiscus discolor* (ocean-spray). Thickets of *Rubus spectabilis* (salmonberry) are found in wet unshaded springs and along streams.

Douglas fir-noble fir community

The east slope (Fig. 2) is forested predominantly with Douglas fir in stands of fairly even-aged trees about 24–36 inches DBH and 125 or more feet tall. This species is predominant on this slope probably because of fire many years ago and also because of rain shadow effects as stated earlier. *Abies procera* is found throughout but is most abundant above 3,400 feet elevation. *Tsuga* occurs only as a few scattered small trees about 24 inches DBH maximum size and these only in the moister locations, near springs and in stream beds. Small trees of *Abies procera* and *Pseudotsuga* are found in more open areas. Seedlings of any kind are rare. The shrub stratum is composed chiefly of a very thick stand of *Gaultheria shallon* with *Berberis nervosa* generally as a secondary plant. Sometimes the latter occurs locally as abundant or more abundant than the former. The upper altitudinal limit of these two species on Mary's Peak is about 3,200 feet, but a few small patches of poorly developed specimens of these plants occur at 3,700–3,800 feet. *Acer circinatum* (vine maple) is quite abundant here in local shaded areas, and *Holodiscus discolor* abundant in the open areas. *Polystichum munitum* (sword fern) occurs in small patches in which it forms almost pure stands.

Douglas fir community

The south and southeast slope is forested more preponderantly with *Pseudotsuga* than the east slope (Fig. 2). It is fairly even-aged, about 24–36 inches DBH, 125 or more feet tall, and forms a dense stand. *Abies procera* is limited to a narrow zone at 3,400 to 3,500 feet on this slope. The shrub layer consists of *Gaultheria* and *Berberis,* which forms a dense ground cover up to about 3,200 feet elevation, which is the upper limit of these plants. There is a zone of *Acer* at 3,400–3,500 feet elevation extending from the west side where the plants are small and very dense, along the south slope, where they are large and dense; to the east slope where the stand thins out. The western part of the south slope and the west slope were burned about 1932, and are now in various stages of succession with *Acer circinatum* and scattered young *Pseudostuga* the only trees. No data were taken from these areas. The small areas of hemlock-Douglas fir in ravines were not sampled. Area exaggerated on map about two times for clearer illustration.

The grassland (meadow) community

The meadow is limited to the top of the mountain and the ridges extending northward and westward (Figs. 3, 4). Grasses are predominantly *Festuca idahoensis* (Idaho fescue) and *Agrostis diegoensis* (bent grass). *Carex californica* (California sedge) is co-abundant with them in many places and most conspicuous during its flowering time in the early part of the season. *Elymus glaucus* forms rather scattered clumps and often small patches. *Phleum alpinum* (alpine timothy) and *Danthonia californica* (oat grass) occur as scattered individuals. *Bromus carinatus* (California brome) is found in places that have been disturbed. *Lupinus albicaulis* (silky-stemmed lupine) and *Delphinium menziesii* (larkspur) are scattered throughout the meadow as conspicuous early plants. The more inconspicuous early flowering species are *Anemone lyallii, Viola glabella, Viola adunca,* and *Collinsia grandiflora.* During June and July, the flowering species include *Calochortus tolmiei* (mariposa lily), *Achillea lanulosa,* and *Senecio in-*

FIG. 4. View north from summit. Present parking area in right background near building at elevation of about 3,700 feet. Trees in midground are a small patch of noble fir. Trees in background are upper part of hemlock-noble fir-Douglas fir community on the north slope. One quadrat line extended from foreground to trees in midground. (Oct. 1947)

tegerrimus. Pteridium aquilinum var. *lanuginosum* (bracken fern) also becomes conspicuous at this time. On the summit region above 4,000 feet elevation is a small area of southwest exposure that receives the full impact of the prevailing westerly winds, causing extremely rigorous conditions. The substratum in this area is almost bare of vegetation and consists of gravel and rock derived from weathered igneous rocks. Here are many clumps of the *Phlox douglassii* (Douglas phlox) and tiny specimens of *Collinsia grandiflora* 1–2 inches high. The more leeward areas of the summit support *Phleum alpinum, Gilia capitata, Koeleria cristata, Lupinus lyallii* (mountain lupine), *Ranunculus occidentalis,* which is also common on pastures and old fields in the valleys, and *Lomatium martindaleyi.*

The meadow is of considerable interest locally because of the intermingling of plants that grow normally at high altitudes and latitudes, those that grow normally only in the drier regions east of the Cascade Mountains, and those plants now common in the drier Willamette Valley. The high altitude species are separated from their normal ranges in the Cascade Mountains by approximately 70 miles. These species include *Phleum alpinum, Arctostaphylos uva-ursi, Phlox douglassii, Lupinus lyallii.* The first two also occur along the coast 35 miles to the westward. The species common to the dry areas east of the Cascades are separated from Mary's Peak by more than 70 miles. Especially notable in this group are *Festuca idahoensis, Carex hoodii,* and *Koeleria cristata.* Species common in the Willamette Valley are at least 10 miles distant from the top of Mary's Peak and separated from it by extensive Douglas fir forest. This group includes *Ranunculus occidentalis, Delphinium menziesii, Collinsia grandiflora, Elymus glaucus, Danthonia californica, Calochortus tolmiei,* and *Lupinus albicaulis.*

Methods

Quadrat analysis of the plant communities on Mary's Peak, above 2,500 feet elevation, supplied analytic data for their description. Quantitative data for the expression of abundance, cover, and frequency were interpreted as described by Braun-Blanquet (1932), and Cain (1932). The qualitative concepts as sociability, periodicity, vitality, and stratification, as described by these authors, were also applied. In addition, the life form as described by Raunkiaer (1934) was determined and is listed for each species, and a life form spectrum for Mary's Peak is compared to the normal and spectra of other areas.

Quantitative analytic concepts

Abundance. These data are intended to express the relative number of individuals of each species entering into the constitution of the plant community. It is based on estimation, and a series of five classes were used (Braun-Blanquet 1932 and Cain 1932).

Class 1—species very rare (very sparse)
Class 2—species rare (sparse)
Class 3—species not numerous (infrequent
Class 4—species numerous (abundant)
Class 5—species very numerous (very abundant).

Cover. This concerns the area covered by or occupied by each species. In several layered tree and shrub communities the cover must be evaluated for each stratum separately because the degree of dominance of a species is given by its share in its layer of the vegetation. One class was added to the five-parted scale of Braun-Blanquet (1932) and Cain (1932) for those plants of very rare abundance and low coverage to emphasize their minor role. These six coverage classes were used essentially as Cain and Penfound (1938), Penfound and Howard (1940) except that 0 was used for the smallest

class of cover. The following coverage classes were used:

Class 0—less than 1% coverage
Class 1—1% to 5% coverage
Class 2—6% to 25% coverage
Class 3—26% to 50% coverage
Class 4—51% to 75% coverage
Class 5—76% to 100% coverage.

The coverage of a species can be measured in each quadrat.

Frequency. This characteristic is concerned with the homogeneity of a stand, or the uniformity of distribution of a species. It is here expressed as a percentage relation between the number of quadrats which contain the species and the total number of quadrats used in the community.

Five frequency classes are used, each with 20 per cent increment, *i.e.,* class 1 includes the species occurring in 1 to 20 per cent of the quadrats, class 2 the species in 21 to 40 per cent of the quadrats, etc.

Qualitative analytic concepts

The qualitative concepts do not require quadrat studies for accurate discernment, but rather depend on as wide experience as possible with the community (Oosting 1948). These concepts are sociability, vitality, periodicity, and stratification.

Sociability. This concerns the grouping or gregariousness of the species in a community. According to Braun-Blanquet (1932) the estimate of sociability is easily made, and on large sample areas it enables one to form a picture of the plant mosaic in much sharper outlines than would be possible from mere abundance and coverage estimates. Cain (1932) states that the assignment of species to sociability classes is subject to considerable variation, the limits of the classes by their very nature being somewhat vague and the personal element entering so largely. The limitation of sociability to five classes helps to standardize these data.

Class 1—growing one in a place, singly, isolated
Class 2—grouped or tufted
Class 3—growing in numbers, small patches, or cushions
Class 4—small colonies, extensive patches
Class 5—great crowds, large colonies.

Vitality. This concerns the degree of vigor attained by the different species in a community. Three classes are usually recognized.

Class 1—Plants germinating but not able to multiply
Class 2—Plants with vigorous vegetative development but not completing their life cycle
Class 3—Plants completing their life cycle.

Most species occurred in class 3.

Periodicity. This refers to the different aspects of the community during the year. The flowering period of plants has been studied and recorded most often and the four classes listed represent this condition of the plants in this paper.

Class 1—prevernal, early spring
Class 2—vernal, spring
Class 3—estival, summer
Class 4—autumnal, fall.

Stratification. This refers to the natural superimposed layers of the vegetation. The vegetation on Mary's Peak has been divided into four strata.

Class 1—tall tree
Class 2—small tree
Class 3—shrub
Class 4—herbaceous.

Immature plants, young trees are referred to as "transgressives" since they are "passing through" the lower strata and will ultimately occupy the higher arborescent stratum (Cain 1932).

In order to be as objective as possible, quadrats must be taken at random (Ashby 1936, 1948). The first may be picked anywhere, then the others at definite in-

tervals along a line (Gleason 1920). In the forest communities, quadrats were located at 50-meter intervals along lines extending up and down the slopes. Those in the meadow followed below or along the ridge crests and extended east, west and north from the summit (legend, Figs. 3, 4). Several sizes of quadrats (¼, ½, 1, 2, and 4 sq. m.) were nested in sets to determine the minimum size necessary to sample adequately the structure of the understory vegetation. These were placed inside 100 sq. m. (10 × 10) quadrats which were used to obtain the tree data (Oosting 1942, Cain 1934, 1935).

Following the interpretation of the species-area curve by Braun-Blanquet (1932), Cain (1938), Hanson and Love (1930), the data indicate that for all communities, quadrats larger than 1 sq. m. would not provide further significant data for herbaceous and shrubby vegetation (Figs. 6–9).

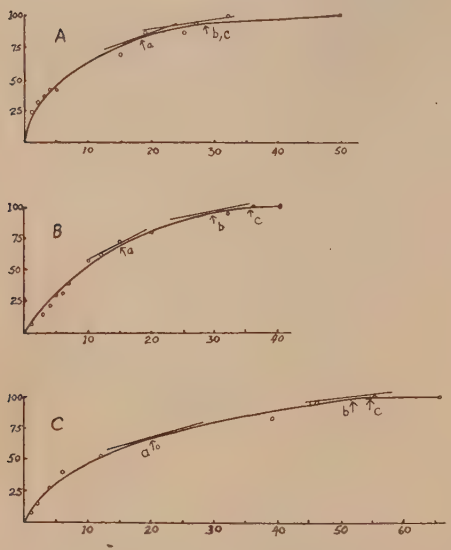


FIG. 5. Graphs indicating the minimum number of 1 sq. m. quadrats necessary to sample the herbaceous and shrubby vegetation of three communities on Mary's Peak. Per cent of species sampled on left side and number of quadrats on horizontal lines. **A**—meadow, **B**—Douglas fir, **C**—hemlock-noble fir-Douglas fir. Arrows indicate minimum number; a—10 per cent rise of species, b—5 per cent rise of species, c—selected by inspection and experience in sampling.

Cain (1938) has pointed out that the shape of the species-area curve, *i.e.*, its flattening, depends on y-x ratio (1–2, 1–3, 1–4, 1–5, etc.) so that the "break of the curve" is shifted in position. As suggested by Dr. Hansen, the per cent of species is recorded here rather than the number of species, so that the same ratio can be used for all communities. Cain (1938) also suggests that a more accurate method is to determine the point at which the curve has a certain percentile rise. His experience indicates that in most cases quadrat size is adequate when there is a 10 per cent increase in species for a 10 per cent increase in area. Greater accuracy can be obtained if the minimal area is placed at the point of 5 per cent increase in species for a 10 per cent increase in area. The minimum size quadrat for all communities was indicated by both the above methods and by inspection.

The next problem was to determine the least number of minimum size quadrats that would yield a representative list of species. This was plotted for the meadow, hemlock-noble fir-Douglas fir, and Douglas fir communities (Fig. 5). The per cent of species was plotted with the number of minimum size quadrats and the resulting curves were examined by the percentile and inspection methods mentioned above.

Discussion of Data

The species-area curves for all communities sampled indicate that the herbaceous and shrub vegetation in all of them would be adequately sampled by the same size of quadrat.[3] By inspection and the point of 5 per cent rise for a 10 per cent increase in area, the 1 sq. m. size is selected. The 10 per cent rise for a 10

[3] No record was kept of the species not sampled; however, all or nearly all the species in each community were sampled by the 1 sq. m. quadrats and are included in the tables.

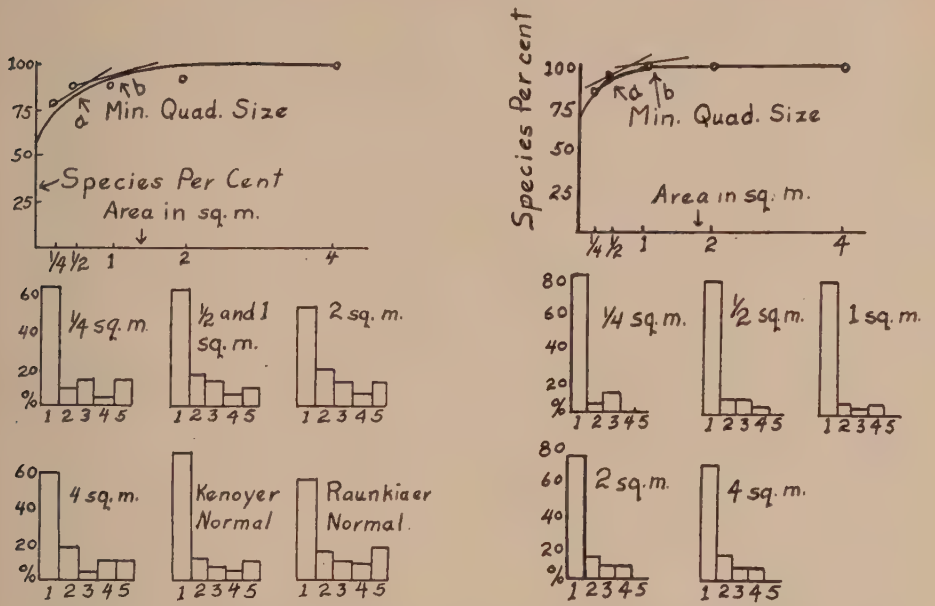


FIG. 6. Graph indicating the minimum quadrat size needed to sample the meadow vegetation; a—10 per cent rise in species, b—5 per cent rise in species and selected by inspection. Also frequency class distribution in the several sized quadrats, based on 50 quadrats, and their comparison with the normals of Raunkiaer and Kenoyer (1927). Height of graphs is based on per cent of species in each frequency class. Class 1 contains species of 1–20 per cent frequency, class 2 contains the 21–40 per cent frequencies, etc.

FIG. 7. Graph indicating the minimum size quadrat needed to sample the understory plants of the Douglas fir community; a and b the same as for Figure 6. Also frequency class distribution in the several quadrat sizes based on 40 quadrats.

per cent increase in area indicates that ½ sq. m. is adequate (Figs. 6 to 9). Hanson and Love (1930) conclude that the minimum size quadrat in grazing studies should be 1, or possibly 2, square meters. The increased cost of larger sizes precluded their use since there were no corresponding advantages. Numerous workers describing various plant communities have generally used quadrat sizes varying from 1/10 to 1 or 2 sq. m. for herbaceous vegetation and up to 4 sq. m. for shrubs and transgressives.

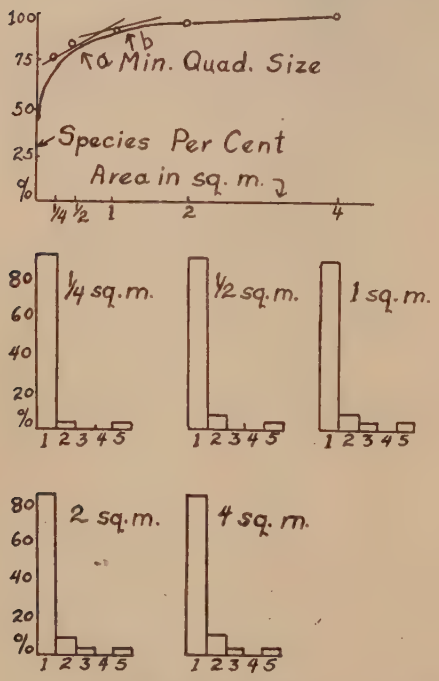
Meadow

The meadow was sampled with 50 quadrats. The species-area curve (Fig. 5A) indicates that a minimum of 20–30 1 sq. m. quadrats is necessary to sample the more important species, and to obtain satisfactory frequency percentages and coverage data. The recorded data and graphs are derived from fifty 1 sq. m. quadrats. Penfound (1945), however, recommends at least ten times the minimum number of quadrats represented by the "break in the curve," which would mean 200–300 on this community. The area here is only about two square miles and I know of no comparative community in western Oregon except possibly on other higher peaks west of the Cascades. The extensive grasslands of *Festuca idahoensis, Poa secunda, Agropyron spicatum,* and *Stipa* spp. east of the Cascades in a drier climate and consequently with less abundance and coverage would certainly require more quadrats for its analysis. However, the curve (Fig. 5A) shows that 80 to 90 per cent

of the species is sampled with the 20–30 quadrats indicated. The graphs show that the frequency of the species is more nearly normal in the 1 and 2 sq. m. plots than any of the others (Fig. 6), indicating that the distribution of the species in this community is relatively homogeneous.

The data place three species, *Festuca idahoensis, Agrostis diegoensis,* and *Carex californica,* in the highest classes of abundance, frequency, and sociability (Table I). These describe their relative numbers as very abundant, evenly distributed over the community, and growing in great crowds or large colonies, respectively. For this reason and by observation each is placed in cover class 4 in considering their sociological status in the community. In some areas each species falls in the highest cover class, although in general two of them, and often all three appeared to have equal coverage. Each species provides a coverage between 50 and 75 per cent giving a total coverage value of over 100 per cent, which can be explained by interfingering of the foliage. All these characteristics combined indicate that these three species are codominant. There is, however, a difference in their periodicity. *Carex californica* flowers in early spring and is more conspicuous at that time than the two grasses. As the season advances the two grasses become more conspicuous and by their flowering time in summer they overtop the sedge, which has matured.

Three other plants, *Elymus glaucus, Achillea lanulosa,* and *Pteridium aquilinum,* were assigned in abundance class



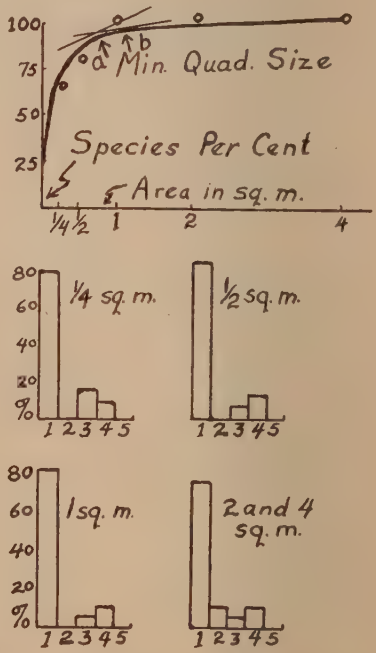


Fig. 8. Graph indicating the minimum quadrat size needed to sample the understory vegetation of the hemlock-noble fir-Douglas fir community; a and b the same as for Figure 6. Also frequency class distribution in the several quadrat sizes based on 65 quadrats.

Fig. 9. Graph indicating the minimum size quadrat needed to sample the understory vegetation of the noble fir-Douglas fir community; a and b same as Figure 6. Also frequency class distribution in the several sized quadrats based on 20 quadrats.

TABLE I. *Data for the meadow on top of Mary's Peak with abundance* (A), *cover* (C), *frequency* (F), *sociability* (S), *periodicity* (P), *stratification* (St), *and life form* (LF) *for each species*

Species	A	C	F	S	P	St	LF
Festuca idahoensis	5	4	5	5	3	4	H
Agrostis diegoensis	5	4	5	5	3	4	H
Carex californica	5	4	5	5	1	4	G
Anemone lyallii	4	0–1	3	3	1	4	G
Pteridium aquilinum	3–4	2	3	3	2	4	G
Viola glabella	3	1	2	3	1, 2	4	H
Elymus glaucus	3	2	2	2–3	3	4	H
Achillea lanulosa	3	2	2	3	3	4	H
Viola adunca	2	0	1	3	1, 2	4	H
Lupinus albicaulis	2	0	1	1	2	4	H
Rumex acetosella	2	0	3	3	1, 2, 3	4	G
Arenaria macrophylla	2	0	1	1	1	4	H
Senecio integerrimus	2	1	1	2	2	4	H
Smilacina sessilifolia	2	0–1	1	2–3	2	4	G
Cerastium arvense	1	0	1	1–2	1, 2, 3	4	H
Danthonia californica	1	0	1	1	3	4	H
Bromus carinatus	1	0	1	1	3	4	H
Fragaria cuneifolia	1	0	1	2	1, 2	4	H
Luzula campestris	1	0	2	2	1, 2	4	H
Collinsia grandiflora	1	0	1	3	1	4	H
Delphinium menziesii	1	0–1	1	1	2	4	H
Melica spectabilis	1	0	1	1	3	4	H
Dentaria tenella	1	0	1	1, 2	1	4	G
Erythronium grandiflorum	1	0	1	1	1	4	G
Phleum alpinum	1	0	1	1	3	4	H
Carex hoodii	1	0	1	1	2	4	H
Erythronium oregonum	1	0	1	1	1	4	G
Arctostaphylos uva-ursi	1	0	1	3	2	3	Ch
Rubus pedatus	1	0	1	1	—	3	Ch

3, cover class 2, sociability classes 2 and 3, and occur in frequency classes 2 and 3. These plants are locally conspicuous, and in a few places the bracken fern may be codominant. They occur in patches and sometimes small colonies scattered over the meadow. *Anemone lyallii* is placed in abundance class 4, and occurs in numbers and small patches fairly well distributed over the community as shown by its inclusion in sociability class 3 and frequency class 3. However, because of its small size it is placed in cover class 0 or possibly class 1. This is one of the smaller, less conspicuous plants and, with other similar sized plants, such as *Arenaria macrophylla, Collinsia grandiflora,* and *Rumex acetosella,* requires careful work for their detection.

Arctostaphylos uva-ursi (bearberry) occurs in one small patch approximately 200 feet in diameter, and one of the quadrats fell near the center of the patch. On this spot the plant is very abundant, completely covering the surface of the ground, and as a small patch is placed in sociability class 3. Concerning the entire meadow community, this plant is reduced to very rare numbers, covers less than 1 per cent of the surface, and occurs in frequency class 1, but retains its sociability class 3 which identifies it as a small local patch of vegetation. The remaining species, mostly in abundance classes 1 and 2, cover classes 0 and 1 frequency class 1, and sociability classes 1 and 2, include the greater number of species which in themselves are not so important, but in the aggregate contribute materially to the completeness of the plant community.

Douglas fir

The Douglas fir community of the south slope was sampled with 40 quadrats. The species-area curve (Fig. 5B) indicates that 15–35 1sq. m. quadrats are

necessary to sample the understory vegetation. The tangent to the curve for 10 per cent rise in species indicates approximately 15, 5 per cent rise indicates 30, and by observation and experience 35 quadrats were selected. The recommendation of Penfound (1945) for 10 times this number could be utilized in the Douglas fir community, because it is very extensive in the Coast Range Mountains and below 2,000 feet elevation on the west slope of the Cascade Mountains. The recorded data and graphs are for the entire 40 quadrats.

The frequency class distribution indicates a rather heterogeneous distribu-

TABLE II. *Data for the hemlock-noble fir-douglas fir community of the north slope of Mary's Peak; legend same as for table I*

Species	A	C	F	S	P	St	LF
Tsuga heterophylla	181*	3	3	4	1	1	Ph
Abies procera	147*	3	3	5	1	1	Ph
Pseudotsuga taxifolia	87*	3	3	1	1	1	Ph
Acer circinatum	41*	0	1	3	1	2	Ph
Thuja plicata	25*	1	1	3	1	1	Ph
Salix scouleriana	4*	0	1	1	1	2	Ph
Taxus brevifolia	2*	0	1	1	1	2	Ph
Fir seedlings (*Abies* and *Pseudotsuga*)	4	0–1	3	3	—	4T	—
Tsuga heterophylla seedlings	3–4	1	2	3	—	4T	—
Vaccinium parvifolium	1	0	1	1	1	4	Ph
Oplopanax horridum	1	0	1	2	2	3	Ph
Rubus pedatus	1	0	1	1	1	3	Ch
Gaultheria shallon	1	0	1	1	2	3	Ph
Berberis nervosa	1	0	1	1	2	3	Ph
Rosa gymnocarpa	1	0	1	1	2	3	Ph
Oxalis oregana	5	4	5	5	1	4	G
Polystichum munitum	3–4	2	2	3–4	—	4	H
Viola glabella	3	1	1	3	1	4	H
Disporum smithii	3	0	1	1	1	4	G
Anemone deltoidea	2	0	1	1–2	1, 2	4	G
Smilacina sessilifolia	2	0	1	1	2	4	G
Achlys triphylla	2	0	1	3	1, 2	4	G
Coptis laciniata	2	0	1	3	1, 2	4	G
Trisetum cernuum	2	0–1	1	1	2	4	H
Montia sibirica	2	0	1	3	1	4	H
Carex mertensii	1	0	1	1	2	4	H
Luzula parviflora	1	0	1	1	1	4	H
Dicentra formosa	1	0	1	1	1	4	G
Trientalis europaea	1	0	1	1	2	4	G
Galium triflorum	1	0	1	1	—	4	H
Vancouveria hexandra	1	0	1	1	1, 2	4	G
Polypodium vulgare	1	0	1	1	—	4	G
Arenaria macrophylla	1	0	1	1	1	4	H
Lomatium nudicaule	1	0	1	1	1, 2	4	H
Listera cordata	1	0	1	1	2	4	H
Viola sempervirens	1	0	1	1	1	4	H
Elymus glaucus	1	0	1	1	3	4	H
Scrophularia californica	1	0	1	2	1, 2	4	H
Senecio triangularis	1	0	1	1	2	4	H
Trillium ovatum	1	0	1	1	1	4	G
Melica spectabilis	1	0	1	1	3	4	H
Clintonia uniflora	1	0	1	1	2	4	G
Mitella ovalis	1	0	1	1	2	4	H
Veratrum californicum	1	0	1	1	2	4	G
Stellaria crispa	1	0	1	1	2	4	H
Unidentified herb	1	0	1	1	—	4	H
Smilacina racemosa	1	0	1	1	1, 2	4	G

* Abundance of trees expressed in actual numbers (density).
T = Transgressives.

TABLE III. *Data for the Douglas fir community on the south slope of Mary's Peak; legend same as table I*

Species	A	C	F	S	P	St	LF
Acer circinatum	290*	3	3	4	1, 2	2	Ph
Pseudotsuga taxifolia	65*	5	5	5	1	1	Ph
Pseudotsuga seedlings	1	0	1	1	—	4T	Ph
Gaultheria shallon	5	4	4	5	2	3	Ph
Berberis nervosa	4	3	4	5	2	3	Ph
Symphoricarpos albus	1	0	1	1	2	3	Ph
Vaccinium parvifolium	1	0	1	1	1	4	Ph
Rosa gymnocarpa	1	0	1	1	2	3	Ph
Achlys triphylla	3–4	2	3	3	1, 2	4	G
Anemone deltoidea	1	0	1	1–2	1, 2	4	G
Galium triflorum	1	0	1	1	—	4	G
Polystichum munitum	1	0	1	2	—	4	H
Montia sibirica	1	0	1	3	1	4	H
Disporum smithii	1	0	1	1	1	4	G
Viola sp.	1	0	1	1	—	4	H
Synthyris reniformis	1	0	1	1	1, 2, 3	4	H
Oxalis oregana	1	0	1	1	1, 2	4	G
Corallorhiza striata	1	0	1	1	2	4	G
Trillium ovatum	1	0	1	1	1	4	G
Dentaria tenella	1	1	1	2–3	1	4	G
Listera cordata	1	0	1	1	2	4	H
Coptis laciniata	1	0	1	2	2	4	G
Arenaria macrophylla	1	0	1	1	1	4	H
Adenocaulon bicolor	1	0	1	1	3	4	H
Osmorhiza nuda	1	0	1	1	2	4	H
Iris tenax	1	0	1	1	1	4	G
Polypodium vulgare	1	0	1	1	—	4	H

* Abundance of trees expressed in actual numbers (density).
T = Transgressives in openings of tree canopy.

tion of the plants because over 80 per cent of the species are in class 1, and the higher classes are very low, with class 5 vacant (Fig. 7).

The even-aged stand of *Pseudotsuga* on the south slope is placed in cover class 5, frequency class 5, and sociability class 5 (Table III). All specimens sampled occur in the largest size class, over 10 inches DBH. The only other tree species is *Acer circinatum* which is quite abundant and occurs in extensive patches. Most of the specimens are in the lowest size class, less than 1 inch DBH. Several, however, are large enough to be placed in size class 3. These larger specimens reach a height of 40 feet.[4] The shrub stratum is composed entirely of *Gaultheria shallon* and *Berberis nervosa,* both abundant, evenly distributed, and in the highest cover class up to about 3,300 feet elevation, which is their upper limit. The change is abrupt with only a few feet vertical distance between a thick stand and a complete absence of these plants. This zone, where these plants are absent, reduces their cover value to 4 for *Gaultheria* and 3 for *Berberis,* and it also accounts for their being in frequency class 4. Above these two species *Montia sibirica* and *Dentaria tenella* are quite abundant, but in the whole community they are rare. Their sociability class 3 indicates they grow in a colony or patch. The remaining plants are those which are infrequent in the community.

Noble fir-Douglas fir

This community on the east slope was sampled with 20 quadrats. The curves for quadrat size (Fig. 9) and number are similar to those of the Douglas fir on

[4] *Abies* was not sampled on this slope because of the impenetrable nature of the thicket of *Acer* in which it was growing. It consisted only of scattered large trees and little reproduction, so had little effect on the community as a whole.

TABLE IV. *Data for the noble fir-Douglas fir community of the east slope of Mary's Peak; same legend as table I*

Species	A	C	F	S	P	St	LF
Acer circinatum	248*	2	3	3	1	2	Ph
Pseudotsuga taxifolia	58*	5	5	5	1	1	Ph
Abies procera	56*	3	3	4	1	1	Ph
Tsuga heterophylla	11*	1	2	3	1	1	Ph
Taxus brevifolia	3*	0	1	1	1	1	Ph
Fir seedlings (*Abies* and *Pseudotsuga*)	1	0	1	1	—	4T	—
Arenaria macrophylla	1	0	1	1	2	4	H
Gaultheria shallon	5	4	4	5	2	3	Ph
Berberis nervosa	5	3	4	4–5	2	3	Ph
Rosa gymnocarpa	1	0	1	1	2, 3	3	Ph
Vaccinium parvifolium	1	0	1	1	1	3	Ph
Polystichum munitum	3	1–2	3	4	—	4	H
Coptis laciniata	2–3	1	2	3	1, 2	4	G
Oxalis oregana	1	0	1	1	1	4	G
Arenaria macrophylla	1	0	1	1	2	4	H
Anemone deltoidea	1	0	1	2	1	4	G
Achlys triphylla	1	0	1	1	1, 2	4	G
Galium triflorum	1	0	1	1	—	4	H
Trisetum cernuum	1	0	1	1	2	4	H
Viola glabella	1	0	1	2	1, 2	4	H
Polypodium vulgare	1	0	1	3	—	4	H
Festuca occidentalis	1	0	1	2	2, 3	4	H
Mitella ovalis	1	0	1	1	2	4	H
Montia sibirica	1	0	1	3	1, 2	4	H
Vancouveria hexandra	1	0	1	1	2	4	G

* Abundance of trees expressed in actual numbers of individuals (density).
T = Transgressives.

the south slope. However, the frequency graphs differ slightly in having class 2 not represented, and class 4 a slightly higher percentage because of fewer total species. Probably insufficient quadrats were taken. *Gaultheria* and *Berberis* are the only representatives in class 4 on both east and south slopes.

Pseudotsuga is placed in cover class 5 and sociability class 5. It occurs mostly as large trees having 78 per cent of the total basal area (Tables IV, VI). The only small trees of this species are in open areas where old trees have fallen. The next most important large tree is *Abies procera* which is most abundant above 3,400 feet. It is represented in all the size classes, especially the smaller. Therefore, with an abundance of only 2 specimens less than *Pseudotsuga* it makes up only 18 per cent of the basal area. *Tsuga* is found only in a couple of ravines on this slope. *Taxus* consists of three small trees in one of the ravines. *Acer circinatum* occurs in small patches of sociability 3.

The predominant understory plants are *Gaultheria* and *Berberis* both about equally abundant and distributed as shown by abundance class 5, frequency class 4, and sociability classes 4–5. *Gaultheria* falls in cover class 4 and *Berberis* in cover class 3, because a well-developed *Gaultheria* plant covers more space than one of *Berberis*. *Oxalis oregana* is unimportant here. *Polystichum munitum* occurs in rather large patches, while *Coptis laciniata* is scattered over the area in small patches. *Festuca occidentalis* (fescue) is a tufted grass growing on the rocky open places in the area. It shows low abundance and frequency, and sociability class 2 indicates its tufted nature. *Anemone deltoidea* is placed in sociability class 2 because its long rhizomes cause the plants to be grouped. The remaining plants may be described as were the less frequent species in the meadow.

Hemlock-noble fir-Douglas fir

This community on the north slope was sampled with 65 quadrats. The species-area curve (Fig. 5C) indicates that 20–60 1 sq. m. quadrats are necessary to sample the understory vegetation. The tangent to the curve for 10 per cent rise in species indicates a minimum of 20, 5 per cent rise indicates about 52 and by inspection 55–60 quadrats were selected. The recommendation of Penfound (1945) for 10 times this number could be utilized in the extensive stands of this type at the higher altitudes (2,000–4,000 or so feet) in the Cascade Mountains. However, here, as in the other communities sampled, the few quadrats used give a picture of the structure and successional tendencies of the vegetation on the limited area at hand. Certainly if information were desired on several hundred square miles of vegetation, *e.g.,* the Douglas fir community of western Oregon, one would naturally need to use several hundred quadrats.

The data for the north slope of Mary's Peak show that *Tsuga* occurs in greatest numbers with 38 per cent of the total abundance (Table II, V). However, the greatest number of specimens are in the small size classes so that this tree has only 14 per cent of the total basal area. *Abies procera* ranks second in abundance with 29 per cent, but first in basal area with 39 per cent because of the larger trees above 3,400 feet elevation. *Pseudotsuga,* with only 18 per cent abundance, ranks close to *Abies* in basal area with 36 per cent. This tree is represented in only the two largest size classes and many of the trees are old specimens often reaching 4 or more feet in diameter, which adds up rapidly in basal area. These three tree species are each placed in cover class 3; *Tsuga,* because it is predominant from 2,500–3,400 feet elevation and rather scattered above; *Abies* because it is dominant above 3,400 feet elevation and more scattered below; and *Pseudotsuga* because of the scattered large trees. The latter is also placed in sociability class 1 for this reason. All three trees fall in frequency class 3. *Thuja plicata* occurs mostly in patches in moister sites around seepage areas. *Acer circinatum* is patchwise in more open areas or in the few places where *Pseudotsuga* provides the canopy. It is not found under *Tsuga* or *Abies. Salix* and *Taxus* grow near the seepage areas and springs.

The most widespread understory plant on this slope is *Oxalis oregana* (Table II). As stated earlier it is so abundant that it often appears as a carpet. Therefore, it is placed in sociability class 5. The sword fern occurs in patches fairly well scattered over the area, especially below 3,400 feet elevation. *Viola glabella* (wood violet) and *Disporum smithii* (fairy bell) are fairly abundant in small patches, but distributed in such a manner that the frequency is low.

TABLE V. *Data used in construction of phytographs of the trees on the north slope*

Species	Frequency	Number in each size class*				Total	Per cent of total	Basal area	
		1	2	3	4			Sq. ft.	Per cent
Abies procera	52	64	11	12	60	147	29	187.12	39
Pseudotsuga taxifolia	52	0	0	36	53	89	18	172.66	36
Tsuga heterophylla	46	68	50	29	34	189	38	64.84	14
Thuja plicata	20	7	4	6	8	25	5	45.50	9
Salix scouleriana	5	0	0	4	0	4	0.8	0.40	1†
Acer circinatum	3	29	12	0	0	41	8	0.24	1†
Taxus brevifolia	2	0	0	2	0	2	0.4	0.33	1†
Total						497		476.09	

* DBH classes as follows: 1—less than 1 inch, 2—1–3 inches, 3—3.1–10 inches, 4—over 10 inches.
† Given value of 1 for plotting purposes.

Seedlings and small trees of *Tsuga* are abundant. Seedlings of *Pseudotsuga* and *Abies* also are abundant. There are no small trees of *Pseudotsuga* indicating inability to multiply and therefore vitality class 1. Small trees of noble fir are quite abundant. *Gaultheria* and *Berberis* are also in vitality class 1 being almost absent on this slope and apparently not flowering. The remaining species have a low abundance, cover, and frequency. Their occurrence in sociability class 1 indicates singly scattered plants and the low frequency indicates their limited numbers and scattered distribution. The data indicate that the flora of the north slope is very heterogeneous and requires a large number of quadrats to obtain a representative sample.

Arborescent Stratum

The analytic data for trees are presented separately in addition to the previous discussion of them in the general treatment of the plant communities. These data were collected in the forest communities from the same number of 10×10 meter quadrats as smaller quadrats in each community. All trees were measured at breast height, and those under one inch in diameter were counted as reproduction and not included in basal area. Seedlings with cotyledons were not counted for this part but were discussed in the data from the smaller quadrats. The data are presented both in tabular and graphic form. The graphic presentation is made by means of phytographs first devised by Lutz (1930). The method consists of a polygonal figure formed on four axes representing the most important criteria for portraying the ecological status of a tree species in a forest community. The four criteria used are abundance, frequency, size class, and basal area. The size classes based on DBH are as follows:

1. trees under 1.0 inch,
2. 1.0 to 3.0 inches,
3. 3.1 to 10.0 inches,
4. over 10.0 inches.

The basal area is the cross sectional area of a tree in square feet determined from the DBH measurement. It was computed only for trees 1.0 inch DBH and over.

These four quantitative factors expressed in the same graph for each species present give an integrated and relative picture of the measurements. The mass effect of the graphs of all the species shows their relative importance in the community.

Hemlock-noble fir-Douglas fir community

The measurements of each species are shown in Table V, and the phytograph for each species shown in Figure 10A. The most important species are *Tsuga, Abies,* and *Pseudotsuga. Tsuga* is the most abundant with 38 per cent of the total, *Abies* next with 29 per cent, and *Pseudotsuga* the least with 18 per cent. All have about the same frequency. *Pseudotsuga* is represented in only the largest two size classes, while *Tsuga* and *Abies* occur in all four. The basal area in this case is the most significant in revealing the ecological relationships of these three species. *Pseudotsuga,* with the lowest abundance, equal frequency, and only two size classes, has 36 per cent of the total basal area. The table and phytograph show that *Pseudotsuga* is lacking in the smaller size classes and, therefore, is not reproducing and will be replaced in this community. *Tsuga,* on the other hand, is the most abundant tree, occurs in all four size classes, but has only 14 per cent of the total basal area, which indicates that it is abundant in the smaller size classes and is reproducing readily. There is also a sufficient number of large trees to consider *Tsuga* a codominant species. The relatively large basal area of *Abies* denotes that there is also an abundance of large trees in addition to the smaller sizes.

The phytograph for *Thuja* suggests that it is a tree of low abundance, fre-

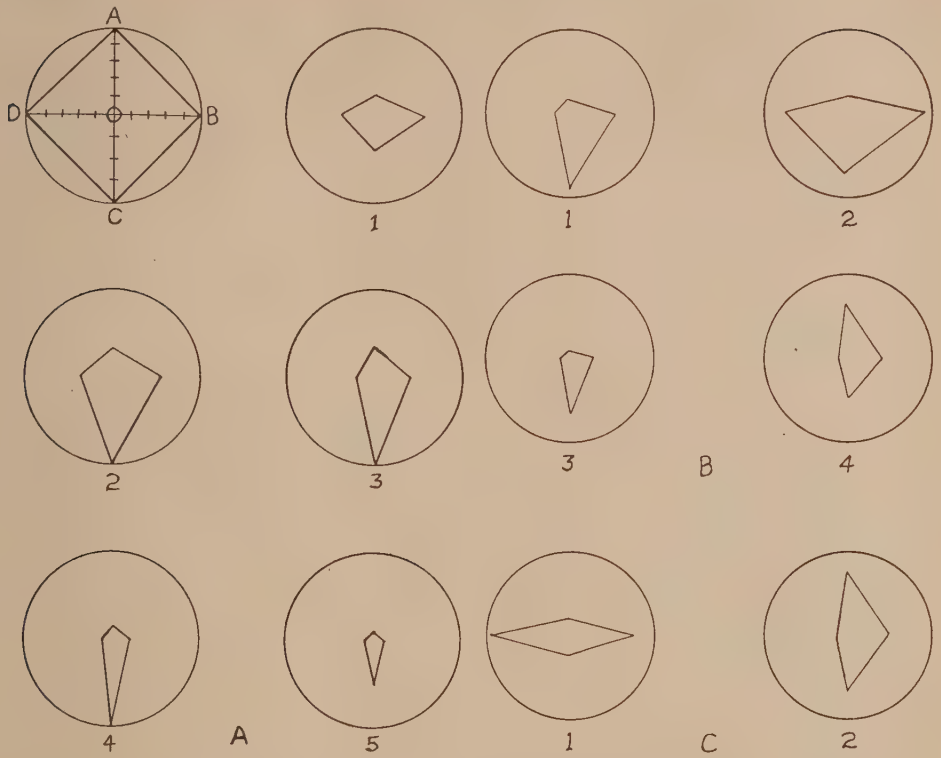


FIG. 10. Phytograph for the major tree species. Key: OA is per cent abundance, OB is per cent frequency, OC is per cent size classes, OD is per cent basal area. **A**—hemlock-noble fir-Douglas fir community: 1—*Pseudotsuga,* 2—*Abies procera,* 3—*Tsuga heterophylla,* 4—*Thuja plicata,* 5—*Acer circinatum.* **B**—noble fir-Douglas fir community: 1—*Abies,* 2—*Pseudotsuga,* 3—*Tsuga,* 4—*Acer.* **C**—Douglas fir community: 1—*Pseudotsuga,* 2—*Acer.*

quency, and basal area. Its occurrence in all four size classes expresses its tolerance of shade and that it is reproducing. It has probably invaded the area much later than *Tsuga.* The phytographs for *Taxus, Acer,* and *Salix* signify the minor and subordinate role of the small tree species under the canopy of the large ones.

Douglas fir-noble fir community

The degree of *Pseudotsuga* dominance on the east slope is shown in Table VI and phytographs in Figure 10B. It has the highest frequency and by far the greatest basal area, and falls in cover class 5. Its extremely large basal area and low abundance with only the 3 largest size classes represented suggest that it is not reproducing under the forest canopy. *Abies,* with the same abundance as *Pseudotsuga,* but a much smaller basal area and occurring in all 4 size classes, is reproducing readily above 3,400 feet elevation, its area of greatest abundance. *Tsuga* occurs only on the moister sites along ravines and is not generally invading the entire slope. As stated earlier, this slope is leeward to the prevailing winds and is drier than the western slope. The small tree species are *Taxus* and *Acer. Taxus* is of negligible importance in the quadrats, consisting of only three trees. *Acer* is most abundant, but nearly all specimens occur in the smallest size class, which makes its basal area negligible.

TABLE VI. *Data used in construction of phytographs of the trees on the east slope*

Species	Frequency	Number in each size class*				Total	Per cent of total	Basal area	
		1	2	3	4			Sq. ft.	Per cent
Pseudotsuga taxifolia	95	0	18	6	34	58	15	171.29	78
Abies procera	60	12	32	7	5	56	15	39.17	18
Acer circinatum	45	201	47	0	0	248	66	0.94	1†
Tsuga heterophylla	35	0	3	3	5	11	3	7.01	3
Taxus brevifolia	15	0	2	0	1	3	0.8	0.89	1†
Total						376		219.30	

* See footnote on table V.
† Given value of 1 for plotting purposes.

Douglas fir community

The data for this community on the south slope are shown in Table VII and phytographs in Figure 10C. *Pseudotsuga* is the only species of the upper arborescent stratum. Its occurrence in a single size class, large basal area, and high frequency indicate large trees evenly dispersed over the slope. The table shows its occurrence in only the largest size class. There were seedlings in the area but no young trees, which supports the statement of Munger (1940) that the seedlings do not survive in the shade of older trees. They will thrive and grow only when an opening occurs in the canopy that allows more light to enter. It is climax, however, because no other species replaces it on these areas. *Acer* is abundant and fairly frequent, but the basal area is negligible. There are some large individuals of this species as shown by 10 specimens in size class 3.

In general, the data from the quadrats in the forest community of Mary's Peak above 2,500 feet elevation indicate that on the north slope *Abies procera* and *Tsuga heterophylla* are codominant and climax, while *Pseudotsuga* is subclimax. On the drier east slope, however, *Pseudotsuga* seems to be codominant and subclimax with *Abies* above 3,300–3,400 feet and dominant and climax below this. On the still drier south slope *Pseudotsuga* is apparently the climax species. Recent burning on the west slope has obliterated any evidence for successional relationships between these three species.

BIOLOGICAL SPECTRUM

The biological spectrum of a region is an expression on a percentage basis of the number of species in each of the life form classes. By means of this spectrum the character of the flora can be presented in table form, can be compared with that of other regions, and thus can be used as an indicator of the climate. The term "life form" was devised by Raunkiaer (1934) and defined as the heritable form

TABLE VII. *Data used in construction of phytographs of the trees on the south slope*

Species	Frequency	Number in each size class*				Total	Per cent of total	Basal area	
		1	2	3	4			Sq. ft.	Per cent
Pseudotsuga taxifolia	86	0	0	0	65	65	18	342.86	99
Acer circinatum	58	248	32	10	0	290	82	1.62	1†
Total						355		344.48	

* See footnote on table V.
† Given value of 1 for plotting purposes.

which the vegetative body of the plant produces as the result of all the life processes which are affected by the environment. The life form allows the use of flora and vegetation as a test of the climate. Similar regions can be compared and dissimilar regions can be contrasted by means of their flora and vegetation. The normal spectrum of Raunkiaer forms an arbitrary base line with which the flora of a region is compared. The class (or classes) with the greatest positive deviation from the normal is taken to indicate the phytoclimate. The value of the spectra lies in the fact that the life forms of the plants of a flora must be considered a reflection and integration of the climatic conditions (Cain 1932). The five general life form classes described by Raunkiaer (1934) and Cain (1932) were used in this study. They are phanerophytes (Ph), chamaephytes (Ch), hemicryptophytes (H), geophytes (G), and therophytes (Th).

The pronounced positive deviation in the hemicryptophytes and geophytes would classify the phytoclimate of Mary's Peak as hemicryptophytic and geophytic (Table VIII). The total of these two classes is 78 per cent of the flora. This may be compared with the flora of Indiana (McDonald 1937), the Olympic Peninsula (Jones 1936), Connecticut (Ennis 1928), and Minnesota (Buell and Wilbur 1948), which show a hemicryptophytic and geophytic content of 60–75 per cent, with below normal percentages of chamaephytes, phanerophytes, and therophytes. The lack of therophytes on Mary's Peak is accounted for by the fact that only mature climax communities were sampled. If recently disturbed areas had been included, several annual species would have been encountered.

The spectrum of the nearby Willamette Valley shows relatively high percentages of geophytes and therophytes. These two life form classes are common in regions with a long dry period. This valley is characterized by a long summer drouth, which is somewhat ameliorated on the higher altitude of Mary's Peak allowing more of the hemicryptophytic forms to survive. That therophytes are predominant on extreme deserts is shown by their high percentage in the spectrum for Death Valley. The spectrum for Spitzbergen at 79° north latitude shows the marked positive deviation of hemicryptophytes and chamaephytes characteristic of the colder climates. The spectrum for the Seychelles, a group of islands in the Indian Ocean, reveals a high percentage of phanerophytes, which is typical of moist tropical climates.

TABLE VIII. *The biological spectrum of the flora of Mary's Peak compared with the normal spectrum of Raunkiaer (1934) and the spectra of other areas*

Region	No. of species	Per cent of species				
		Ph	Ch	H	G	Th
Normal spectrum	1000	46	9	26	6	13
Mary's Peak, Oregon	124	19	2	54	25	0
Willamette Valley, Oregon	600	11	2	30	24	33
Olympic Peninsula, Washington	1015	11	6	52	22	9
Connecticut	1453	15	2	49	22	12
Indiana	1837	15	2	50	20	13
Minnesota	145	36	3	44	17	0
Death Valley	294	26	7	18	7	42
Spitzbergen	110	1	22	60	15	2
Seychelles (tropical)	256	61	6	12	5	16

SUMMARY

Data were obtained on Mary's Peak in western Oregon during the summer of 1947 to evaluate the application of the several phytosociological concepts concerned in the analysis and description of plant communities. These concepts are based largely on quantitative and qualitative characteristics. Quantitative characteristics are abundance, coverage, and frequency. For trees, basal area and size classes computed from field measurements of diameter at breast height were also considered. Qualitative characteristics include sociability, vitality, layering, periodicity, and life forms. The results are presented in tables and graphs.

Mary's Peak (elev. 4,097 feet) is the highest in the Coast Range Mountains between the Olympic Mountains in Wash-

ington and the Klamath Mountains in southwestern Oregon. The Coast Range of Oregon has a wet, microthermal climate with precipitation adequate at all seasons. The proximity to the Pacific Ocean causes a distinct marine climate.

Mary's Peak lies within the cedar-hemlock association of the coast forest. The north slope is covered predominantly by *Tsuga heterophylla* (western hemlock), *Abies procera* (noble fir), and *Pseudotsuga taxifolia* (Douglas fir). *Tsuga* is most abundant from 2,500 to 3,600 feet elevation, and ranges in size from seedlings to about 24 inches DBH. *Abies* is most abundant above 3,500 feet and above 3,700 feet forms a pure stand with size ranges from seedlings to about 50 inches DBH. Below 3,500 feet it becomes scattered and below 2,500 feet it is very sparse. *Pseudotsuga* is frequently represented by scattered giant specimens 45–60 inches DBH, in addition to smaller trees up to about 3,500–3,600 feet. Above this, to about 3,700 feet which is its upper limit, the largest trees are only about 18–20 inches DBH.

Thuja plicata (western hemlock) occurs mainly on moister sites about springs and along streams up to about 3,500 feet. Trees of negligible importance are *Taxus brevifolia* (yew), *Acer circinatum* (vine maple), and *Salix scouleriana* (willow).

Tsuga, Abies, and *Pseudotsuga* each occur in frequency class 3 (41–60 per cent of the quadrats), and cover class 3 (covers 26–50 per cent of the ground). *Tsuga, Abies,* and *Thuja* occur in all 4 size classes, while *Pseudotsuga* occurs only in the largest 2 classes. *Tsuga* has 38 per cent of the total individuals and 14 per cent of the basal area, *Abies* has 29 per cent of the individuals and 39 per cent of the basal area, and *Pseudotsuga* has 18 per cent of the individuals with 36 per cent of the basal area. This indicates that the first two are climax with *Thuja* and are maintaining their position, but *Pseudotsuga* is subclimax and not effectively reproducing in the shade of the forest. It is being replaced by the other species. Phytographs are presented for the tree species.

A shrub layer is almost non-existent here, except for scattered patches of *Gaultheria shallon* (salal) and *Berberis nervosa* (Oregon grape) under *Pseudotsuga.* The herbaceous layer is composed largely of *Oxalis oregana* (wood sorrel) which occurs in abundance class 5, cover class 4, frequency class 5, and sociability class 5. It often forms a "carpet" except under *Tsuga* where a litter (1–3 inches deep) of leaves and twigs apparently prevents the growth of other plants.

A total of 45 species was sampled with 65 small quadrats nested in 10 × 10 sq. m. quadrats used for the trees. The species-area curves indicate that 1 sq. m. is the minimum size necessary for the understory and that 20–60 of them would adequately sample this community.

The east slope is forested predominantly with *Pseudotsuga,* particularly below 3,500–3,600 feet elevation, which consists of fairly even-aged trees about 20–30 inches DBH. Small trees are found only in openings among larger trees. Above this elevation, *Abies* is codominant with *Pseudotsuga* and more abundant in the lower size classes. *Pseudotsuga* is included in the highest frequency, cover, and sociability classes, in the 3 largest size classes, has 15 per cent of the total tree abundance, and 78 per cent of total basal area. *Abies* is included in frequency class 3 (60 per cent of the quadrats), cover class 3, sociability class 4, in all 4 size classes, 15 per cent of total tree abundance, and only 18 per cent of the total basal area.

Tsuga occurs only in ravines and spring areas as a few scattered small trees about 24 inches DBH maximum size. It is included in frequency class 2, cover class 1, sociability class 3 (small patches), and 3 per cent of the total abundance and basal area. It undoubtedly will never replace the above species on this slope, which is less mesic due to the rain shadow effects from the prevailing westerly winds. *Acer circinatum* is the most abundant tree in numbers with 66 per cent of the total, but

its basal area of less than 1 per cent is negligible. It is included in frequency class 3, cover class 2, and sociability class 3. It occurs in only the 2 smallest size classes.

The shrub layer is composed mainly of a very thick stand of *Gaultheria shallon* (salal) and *Berberis nervosa* (Oregon grape), generally up to 3 feet tall. These two species are included in abundance class 5, cover classes 4 and 3, frequency class 4, sociability class 5. Their upper altitudinal limit is about 3,200–3,300 feet, except for a few small patches above this. The herbaceous layer is sparse and of low value in all characteristics. A total of 25 species was sampled with 20 quadrats. Small quadrats for the shrubs and herbs were nested in 10 × 10 sq. m. quadrats for the trees.

The south and southeast slope is forested more preponderantly with *Pseudotsuga* than the others sampled. It is fairly even-aged, 20–36 inches DBH, and occurs only in the largest size class. It is included in the highest cover, frequency, and sociability classes. Reproduction of this species is occurring only in openings in the forest. Compared to *Acer* it has only 18 per cent of total abundance, but nearly 100 per cent of the basal area. The only other tree sampled, *Acer,* is very abundant, is included in the lower 3 size classes, cover and frequency class 3, and sociability class 4 (large patches). *Abies* was not sampled here because it was only a narrow band of scattered trees growing in an impenetrable thicket of *Acer* above and not influential on the community as a whole. The shrub layer is similar to that of the east slope. The herbaceous plants are generally sparse and scattered, and occur in the lower classes of the characteristics used. *Achlys triphylla* (vanilla leaf) and *Melica subulata* (onion grass) are the most important. They are included in abundance class 3, cover class 2, frequency classes 3 and 2, and sociability classes 3 (small patches) and 2 (tufted) respectively. A total of 27 species were sampled with 40 small quadrats for the understory nested in 10 × 10 sq. m. quadrats for the trees. The species-area curves indicate that 1 sq. m. is the minimum size for the understory vegetation and that 15–35 of them would adequately sample this community and that of the east slope.

The west slope was burned over about 1932. No data was obtained from this area which is in various stages of succession depending on elevation and exposure.

The summit and ridge tops to the extent of about 2 square miles is covered with a meadow. It is composed of a quite thick and continuous cover of *Festuca idahoensis* (Idaho fescue), *Agrostis diegoensis* (leafy bent grass), and *Carex californica* (California sedge). Each is included in the highest classes of abundance, frequency, and sociability, and in cover class 4. They were considered co-dominant, but *Carex* is more conspicuous during its flowering period in May and early June, but from July on it is overtopped by the grasses. *Elymus glaucus* (wild rye) and *Pteridium aquilinium* (bracken fern) form small patches scattered over the area.

The early spring flowering aspect includes *Lupinus albicaulis* (lupine), *Delphinium menziesii* (larkspur), *Anemone lyallii* (wind flower), *Viola glabella* (wood violet), and *Collinsia grandiflora* (large innocence).

The summer (June, July) aspect is furnished chiefly by *Calochortus tolmiei* (mariposa lily), *Achillea lanulosa* (yarrow), and *Senecio integerrimus* (tall ragwort).

A total of 29 species were sampled with 50 quadrats. The species-area curves indicate that 1 sq. m. is the minimum size necessary and that 20–30 of them would adequately sample this community.

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ECOLOGIC OVERLAP AND INTERSPECIFIC STRIFE IN BREEDING POPULATIONS OF ANNA AND ALLEN HUMMINGBIRDS

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Analyses of interspecific competition in natural populations are fundamental to modern theory in ecology and evolution. Yet, at least among higher vertebrates, few examples with supporting details are on record, and current theories require corroboration in the field (Errington 1946; Crombie 1947; Richards 1948; Lack 1949). This will come slowly, chiefly because the proper recording and interpretation of competitive incidents in the field require a long and intimate field acquaintance with a given species and because the details of such incidents are often elusive or subtle. Also, the true nature of adaptive differences between closely similar species may escape detection unless these are observed in competition (Lack 1944; Crombie 1947). The object of this paper is to examine ecological differences between two sympatric species of hummingbirds which overlap in both geographic and habitat distribution, providing an example of what, in Schmalhausen's (1949) classification of competitive situations, is termed "active intergroup competition."

The Anna hummingbird (*Calypte anna*) and the Allen hummingbird (*Selasphorus sasin,* formerly *S. alleni*) are almost restrictedly Californian in breeding distribution, and their breeding ranges overlap along the coast from the San Francisco Bay region to Ventura County (Grinnell and Miller 1944). The evidence to be presented here was obtained in the course of a five-year census, in the period from 1943 to 1947, of the breeding population of hummingbirds in Woolsey Canyon, which drains into Strawberry Creek on the west side of the Berkeley Hills. The study area, now a part of the University of California campus, totals about 125 acres and, until 1948, supported a complex of woodland and chaparral vegetation surrounded by open grassy slopes such as typically fills the canyons in the central Coast Ranges (see Fig. 1). Studies of territoriality in hummingbirds reported earlier (Pitelka 1942) have been continued, and while data presented in this paper concern specifically the populations of Woolsey Canyon, much original information on behavior to be reported elsewhere has been used in interpreting the data on these populations.

MORPHOLOGICAL CHARACTERS

The two genera, *Calypte* and *Selasphorus,* are considered by avian taxonomists to be closely related (Ridgway 1911; Peters 1945). The two species under study here, *C. anna* and *S. sasin,* resemble numerous other trochilid species in general form and in general type of coloration (Ridgway 1892). The important differences between them, here described only briefly, are apparently all adaptively significant.

In *anna,* the throat iridescence extends on to the crown, and this extension has evidently evolved as an enhancement of the flash effect which the iridescence produces at the end of the deep dive and in the sharp upturn of the characteristic flight display of this species. The tail is rounded in *sasin;* in *anna* it is emarginate in males, rounded in females. This difference, and also those of the shape of the outermost tail feathers and primaries of the males of the two species, are related to differences in style of flight-display. In coloration, *anna* is darker than *sasin,* and the greens in particular are duller. This correlates with differences in background color of habitat, *anna*

occurring in chaparral and evergreen woodland, *sasin* in areas of deciduous shrubs with softer, brighter foliage.

In size, *anna* is larger than *sasin* (Table I). This difference, considered as a general interspecific one, suggests the operation of Bergmann's rule (Allee *et al.* 1949). *Anna* is permanently resident on its breeding range, which is more or less coincident with the region of winter rains in the central valley of California and along the coast from the San Francisco Bay region south into northern Baja California (Grinnell 1928; Grinnell and Miller 1944). *Sasin* is only a summer resident of restricted distribution along the Californian coast (Grinnell and Miller 1944). Bergmann's rule, strictly interpreted, applies only to *intra*specific variation; but considering general similarities of *anna* and *sasin* in both structure and ecology, that rule may be relevant to the observed size difference between the two species. The known ecology of the two species suggests no additional possible explanation.

FIG. 1. Map of Woolsey Canyon, west side of Berkeley Hills, Alameda County, California. Oak-laurel woods are inclosed by a heavy line. The grid of broken lines indicates acres. Elevation intervals of 200 feet are shown by thin lines.

From Table I, it is evident that the degrees of sexual dimorphism are not the same in the two species; if we take *anna* as 100 per cent, *sasin* is smaller by the following percentages:

	Males	Females
Wing	21.7	7.2
Culmen	17.0	2.5
Weight	26.9	11.5

In both species, males are smaller than females in all characters studied except that in *anna*, females evidently weigh less than males. This seeming inconsistency requires corroboration. If it is real, it may be related to genetic balances between these and other characters in the females of the two species which resemble each other more than do the males. Thus, in both wing and culmen, females differ less than males, and correlated evolutionary adjustments in body mass may lead to the observed reversal of difference in average weight of the sexes of *anna*. It should be noted that females of *anna* and *sasin* also resemble each other more in plumage characters than do males.

Of the mensural characters studied, *anna* and *sasin* differ least in size of bill. The resemblance carries to form of bill (Ridgway 1911) and to feeding habits. Both species take small insects and spiders as well as nectar. No quantitative data on kinds of food eaten are available, but if any significant interspecific differences exist, none has been suggested by extensive field observations of both species, except that *anna* males may do more flycatching from their lookout posts than

TABLE I. *Measurements of* Calypte anna *and* Selasphorus sasin[1]

	Sex	Number of specimens	Range	Mean with standard error	Standard deviation
C. anna					
Wing	Males	22	47.0–50.1	48.87 + 0.16 mm.	0.76
	Females	13	49.0–51.3	50.14 + 0.15	0.53
Culmen	Males	22	15.9–18.3	17.06 + 0.16	0.73
	Females	12	16.3–19.1	17.43 + 0.27	0.94
Weight[2]	Males				
	Apr.–Sep.	7[3]	3.3–4.7	4.00 grams	
	Oct.–Mar.	6[3]	3.5–4.7	4.20	
	Dec.–Apr.	8[4]	3.4–5.5	4.45	
	Females				
	Apr.–Sep.	7[3]	3.1–4.9	3.81	
	Oct.–Mar.	6[3]	3.2–4.7	3.68	
S. sasin					
Wing	Males	15	37.5–39.1	38.26 + 0.11 mm.	0.44
	Females	11	39.7–42.6	41.64 + 0.25	0.83
Culmen	Males	12	14.9–16.9	15.83 + 0.16	0.56
	Females	9	16.2–17.3	17.00 + 0.16	0.47
Weight[5]	Males	7	2.7–3.6	3.10 grams	
	Females	4	3.2–3.5	3.32	

[1] All specimens for linear dimensions collected near east shore of San Francisco Bay (Hayward, Oakland, Berkeley).

[2] Additional data provided by O. P. Pearson suggest that the normal daily weight variation in *anna* and *sasin*, which, like other hummers, feed frequently, is probably not more than 5 to 10 per cent of the maximum weight in a given individual.

[3] Specimens collected in coastal California.

[4] Specimens collected in northern Baja California.

[5] Specimens collected in central and southern coastal California, March to August.

sasin males. Whatever differences in feeding efficiency may occur, the fact remains that both *anna* and *sasin* have been observed numerous times using identical food sources.

C. anna and *S. sasin* are known to hybridize occasionally. Of four known male specimens, three were collected in the San Francisco Bay region (Taylor 1909).

In summary, *C. anna* is larger than *S. sasin*. Males of both *sasin* and *anna* are smaller than their respective females, at least in size of wing and culmen. Interspecific differences are greater in males than in females (a situation not uncommon in various groups of birds, but the quantitative expression of those differences may bear upon sexual differences in habitat distribution discussed beyond). Most of the recognized morphological differences can be assigned an adaptive significance related to behavior or habitat. Among characters considered, the two species differ least in feeding equipment and feeding behavior.

HABITAT PREFERENCES AND TERRITORIALITY

1. Males of Calypte anna

In *Calypte anna,* a permanent resident throughout its range, the period of most active territorial occupation occurs from December through April (Fig. 2). In Woolsey Canyon, males occupied territories in areas of broken vegetation, usually chaparral with scattered broad-leafed evergreen trees (*Quercus agrifolia* and *Umbellularia californica*) in or adjacent to woodland areas. Territories were also held along stream courses in areas of large willows bordered and undergrown with various shrubs. These latter terri-

tories also included at least occasional oaks or laurels growing near or within the willow areas. A male typically had one or two favorite, prominent perches, or territorial posts, which overlooked the shrubs and most of the trees of his territory and from which he sang and initiated flight-displays. Each territory neighbored an open more or less grassy area, and almost all territories were on slopes so that each male had a vista of not only the shrubby area immediately below and around his post, but a considerable peripheral open space around *and above* the center of the territory where most of the activity occurred. These parts of a male's living space which received territorial attention may be termed, respectively, the buffer area and the core area.

The core area represents the part of a territory defended at all times of the year by the male which remains on it continuously (see examples for 1943–44, Figs. 5 and 6). It also represents the minimum area defended in the non-breeding season by either immature or adult males in sites other than those used for breeding territories. In size the core area averages ¼ acre (or about 100 × 100 feet). In the non-breeding season this area is usually smaller, whereas in the breeding season it is occasionally a half-acre, as when a male has two rather widely separated but regularly used territorial posts (for example, 1944, male 4, and 1945, male 2).

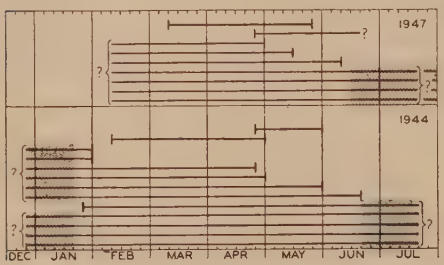

FIG. 2. Seasonal site-occupancy by territorial males of *Calypte anna,* Woolsey Canyon, 1944 and 1947. Each heavy line represents occurrence at one site. Vertical lines indicate, within five-day periods, first or last records at sites not occupied at time of earlier or later observation. Dots indicate periods within which first or last observations of a season were made and signify only that sites were then occupied. Queries also indicate sites occupied before first or after last observation.

The buffer area, or better, buffer space, surrounds the core area and is actively defended only in the breeding season. Intruders entering this area will be challenged and chases of intruders from any part of a territory usually continue through the buffer area. But regular song, display, and announcement flights are confined to the core area. The size of the territory, or the combined buffer and core areas, may be estimated at six to ten acres; but it should be emphasized that the outer limits of the buffer area vary considerably, depending usually on habitat features and on proximity of other territorial males. Overlap may occur in buffer areas of closely neighboring males.

These approximations are based on observations of a minimum of 48 areas held in the five breeding seasons in Woolsey Canyon and on additional areas on and near the campus of the University of California. Difficulty is encountered in setting the limits of the core area of a given male, but this in itself is not a serious handicap to estimating size of territories when observations on a number of other males are also made. But this difficulty means that the areas outlined on the maps exceed the core areas and include parts of adjacent buffer areas where perches were available near to a male's main or "home" perches and where some type of territorial activity other than chases or challenge flights was observed. Thus, for the Anna hummingbird, the boundaries shown on the maps delimit total areas where primary territorial activities such as singing, displaying, announcement-flights, and defense-flights occurred. Those boundaries also encompass minor shifts in core areas; any major shifts that were detected are indicated separately (for example, see change in areas occupied along Upper Draw in 1943, Fig. 5).

In the breeding season, song is regu-

larly delivered from territorial posts in the core area and also on wing in circuit flights, which are here termed announcement flights, and in challenge flights out over the buffer area toward a neighboring male. Dive displays are performed typically over the core area, rarely in the buffer area or in the core area of a challenged, resisting neighboring male. Flights to challenge and chase away intruders, even those merely flying over a territory as much as 40 or 50 feet above the ground, are made into the buffer area as well as to all parts above and within the vegetation of the core area. These defense flights are often accompanied by song. Chases of intruders may continue several hundred feet beyond the limits of the buffer area and occasionally over the territory of a neighboring male.

Established males are aware of their neighbors and in the breeding season there is an intermittent but recurrent testing of one established male's territorial defense by his neighbors, especially when their respective activities are easily evident to each other. This apparently leads to occasional displacements even in the breeding season (for example, see summary of data for 1943 and relations of male 7 to neighbor's territory). Also, it is evident that if an area is vacated, this is promptly discovered by neighboring males, one of whom may take it over. This interpretation would allow for the fact that of 12 sites used by breeding males in Woolsey Canyon, nine were used in four or five seasons and three were used in but two seasons. It is true that some first-year males probably settled down on breeding territories later than December or January and that these could have taken over vacated sites in intervals between my records. But I believe that the summated records indicate some shifting of territorial males, for were the occupation of a given territory more a matter of the survival of one male present at the beginning of the season, it seems unlikely that nine of the suitable areas would be occupied so consistently.

Territorial activity subsides in late May and early June. Announcement flights and challenge flights become infrequent and no longer occur when a male confines himself to a core area or moves to woodland or to other areas used as feeding territories. Song becomes irregular and dive-displays occur infrequently. Through the summer and fall, local movements on the part of individuals are frequent, and territorial activity centers around small feeding and resting areas which may be occupied for varying periods of time. This applies more to immature males than to adult males, which tend to remain in the vicinity of favored breeding territories, if not in the core areas; but even they at times absent themselves from these areas. Shifts in territorial occupation probably occur among locally resident males at this time; probably no more than three of the areas occupied in the summer and autumn of 1943 were held by the same males through these seasons.

After the annual molt, which in resident males occurs from late June until August, singing occurs irregularly, but on occasion, for periods of up to 15 to 30 minutes, singing is regular. Such periods become more frequent and average longer as the season of winter rains approaches. Diving occurs occasionally and in certain individuals only. With the first heavy winter rains, changes in the local distribution of Anna hummingbirds are more abrupt than at any other time of the year. The increase in frequency of song and display, otherwise more or less gradual through the fall, is abrupt at this time, at least with certain individuals. It continues into December or January, by which time locally resident males, if they are not already settled on suitable breeding habitat, shift to such areas.

2. *Males of* Selasphorus sasin

In *Selasphorus sasin,* the picture of territoriality is simpler. The species is a summer resident throughout its range

(Grinnell and Miller 1944, p. 221) and, in the San Francisco Bay region, occurs from February until October. Males take up territories from mid-February until mid-March and leave them from mid-May to mid-June (Fig. 3). Flight-displays of territorial males were recorded in Woolsey Canyon from February 13 to June 15 (Fig. 4). The wings of males produce a sound additional to the usual hum which serves to announce presence of a male and which functions in this manner in circuit flights over a territory. Notes of males, although they are merely chips or chatters like those of females and young, are used in announcement, but relatively infrequently. There is no characteristic song.

The breeding territories of males, in the Berkeley Hills, are typically held along canyon bottoms or along stream courses, in areas of massive, deciduous shrubs, usually willows, often poison oak or dogwood. A prominent twig overlooking the shrub mass is used as a territorial post. This may be a high twig of the willows, or it may be a lateral, exposed branch of an oak, laurel, or other tree from which the hummer oversees the shrub mass. Areas of suitable breeding territory are typically more or less widely separated and more or less inclosed by trees or bordered by open grassy slopes. Intraspecific territorial encounters, at least so far as observations in the Berkeley Hills show, are not so frequent in *sasin* as in *anna*. Moreover, males of *sasin* guard the shrub area, chase intruders from it, display over it, perform circuit or announcement flights over it, but only the shrub area and the open space 10 to 15 feet above it are defended. Unlike *anna*, therefore, there is no attention to space or to other hummers beyond what corresponds to the core area in *anna*. There are no challenge flights addressed to neighbors, no patrolling of buffer areas, no challenges and chases in buffer areas lateral to or above the core area. When territorial squabbles have been observed between closely neighboring males, they were challenges, chases, and announcement flights all more or less oriented with reference to a boundary (for example, see Fig. 5), and the two males observed this boundary in the manner common to such passerines as song sparrows or Bewick wrens. In other words, there is not the overlap conspicuous in the territorial behavior of *anna*, and there are no recurring invasions and counter-invasions between neighboring territories.

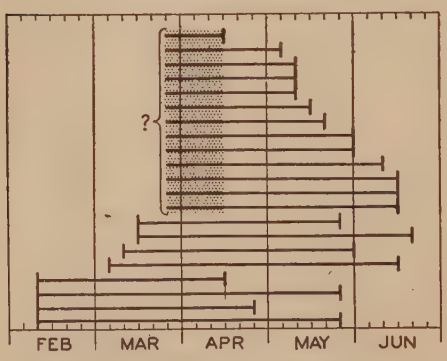

FIG. 3. Seasonal site-occupancy by territorial males of *Selasphorus sasin*, chiefly in Woolsey Canyon, 1943–1947. Each heavy horizontal line represents occurrence at one site. For explanation, see legend of Figure 2.

Males of *sasin* have been observed in the breeding season in areas of female nesting habitat, displaying there or not, but in any case remaining briefly and not holding territorial posts. The evidence, which is scattered, circumstantial, but consistent, suggests that in the mating period the brief pair-bond may draw the male from his territory at least intermittently to a nearby nesting area.

From these summaries, the following basic points concerning male territoriality are evident. Males of *anna* are established on their territories usually at least a month in advance of males of *sasin*. The spatial requirements of *anna* are greater than those of *sasin*. The habitats of the two overlap to the extent that certain vegetation areas required by *sasin* may be included in the habitat of *anna* if features of adjacent areas are also suitable.

3. *Females of both species*

In both species, females nest in habitats other than those used by males as breeding territories (Grinnell and Miller 1944, pp. 220, 222). In natural areas of the Berkeley Hills, females of *anna* usually nest in live oak trees in groves or in more or less continuous woodland. Females of *sasin* nest in oak-laurel woodland, in understory shrubs such as blackberry or thimbleberry, or in thickets of deciduous shrubs such as willows, or in areas of mixed tall, soft and more or less broken chaparral with scattered trees such as occur on extensive north-facing slopes. This habitat separation of the sexes, which occurs to varying degrees among the North American species of hummingbirds, is a corollary of the fact that the pair-bond, if indeed one is formed, apparently exists only in the period of mating (Pitelka 1942, p. 195).

4. *Young of both species*

Immature males of *anna* become territorial toward the end of the breeding season, in mid-May, with the result that they aggravate local territorial stress and probably accelerate the breakdown of at least certain territories occupied by adults. Immature males sing and display, with obvious inexperience but with a persistence at least comparable to that in the waning territoriality of adult males. Territories are small and comparable to the core-areas of adult males; moreover, they are held temporarily, usually no more than for hours or days and occasionally for some weeks (for example, see Fig. 6).

In *sasin,* by mid-June, and with the onset of the dry season, numbers in the Berkeley Hills fall off and only occasional individuals, most of them probably immature, are seen (see examples, Fig. 6). Concentrations of *sasin* hummingbirds are to be seen about garden plantings through the summer and into October, but under primitive conditions in central coastal California there must have been more of a general post-breeding exodus of this species from areas away from the immediate coast than is true today. This is true in less disturbed areas, as in interior Monterey County (Linsdale, 1947, p. 238). At any rate, by July, the hummingbird population in such an area as Woolsey Canyon includes only a small number of *sasin* hummingbirds. Most of them wander locally and are present only briefly at a site of observation, whereas most adult males of *anna* are locally resident, and immature males, if they are not locally resident, tend at least to linger in the area more than young of *sasin* (see Fig. 6).

Breeding Seasons

Nesting records for the San Francisco Bay region have been compiled from my notes, various ornithological journals, and original notes deposited by other observers in the Museum of Vertebrate Zoology. The available data are graphed in Figure 4. With two exceptions, the records for *anna* come from localities on the east side of San Francisco Bay; those for *sasin* come from various parts of the region. Because ornithologists tend so faithfully to put on record what is extreme, marginal, or extralimital, we can be reasonably certain that the limits recorded in Figure 4 easily include the breeding activity of most years. More extensive data collected near Santa Barbara, California (Pitelka 1951), also support this conclusion.

From Figure 4, it is evident that the breeding season of *anna* begins in late December whereas that of *sasin* begins in early February. One set of eggs of *anna* found on January 14 in Oakland was about to hatch then. As the incubation period is usually 16–17 days, and as we may allow a week for nest-building, this nesting probably began between December 20 and 25. Two nestings per season typically occur in both species; it is probable that in *anna,* three occur occasionally. In both species, almost all breeding activity is concluded by mid-July.

Thus, the breeding season of *anna* be-

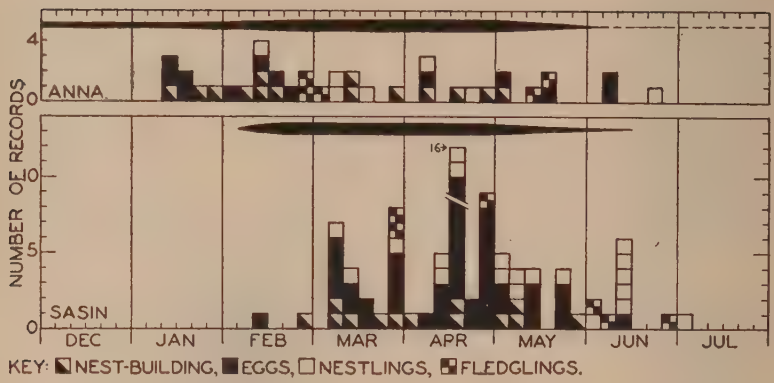

FIG. 4. Breeding seasons in *Calypte anna* and *Selasphorus sasin* in the San Francisco Bay region (see text). Each nesting record (39 in *anna*, 85 in *sasin*), from whatever phase of the cycle, represents one nesting. Occurrence of territorial flight-display in males shown by bars above breeding records; broken line signifies display occurs, but only rarely.

gins four to six weeks ahead of that of *sasin*. From this evidence and also that on territoriality in males summarized above, it is clear that in areas of habitat overlap *anna* has an advantage in that at least that segment of the population beginning its breeding in the first month of the season does so without immediate relation to *sasin*.

Collection and Use of Data

The evidence on interspecific strife reported here was an unexpected by-product of a five-year survey of populations of breeding birds in Woolsey Canyon. Some 300 hours were spent there on 78 different days in the years from 1943 to 1947. About 80 per cent of this time was spent in the field from mid-March to mid-July. Systemic observations were continued throughout the year only in 1943. Hummingbirds observed in the course of each census were located on maps separate for each resident species. Results of five successive censuses were recorded on one map for resident species. For non-resident hummers and for *Selasphorus* hummers in the non-breeding season, observations were recorded in the field on maps separate for each date. The extent and quantity of population data may be judged from Figures 5–8 (see legend of Fig. 5). During censuses, activities of hummingbirds were observed and recorded when they appeared to yield critical items of information on behavior, and the most important of these bearing on interspecific relations are cited in the summary concerning identity of individuals however, at any given time or place rarely exceeded a half-hour because it was not relevant to the main objective of the field work in Woolsey Canyon and because it was mostly corroborative to observations on hummingbird behavior recorded elsewhere in the same period.

While each male occupying a given site, as shown in Figures 5–8, is given a number for the purpose of convenient reference, it should be clear that I have no proof that the *same* individual was present through the entire period that the site was occupied. It is only my opinion that most of the sites occupied through a breeding season by both *sasin* and *anna* were each held by one individual. This is strongly suggested by various details of behavior one notes through repeated observation of a given individual. The likelihood of some shifts among occupant breeding males of *anna*, however, has already been discussed above. I draw no

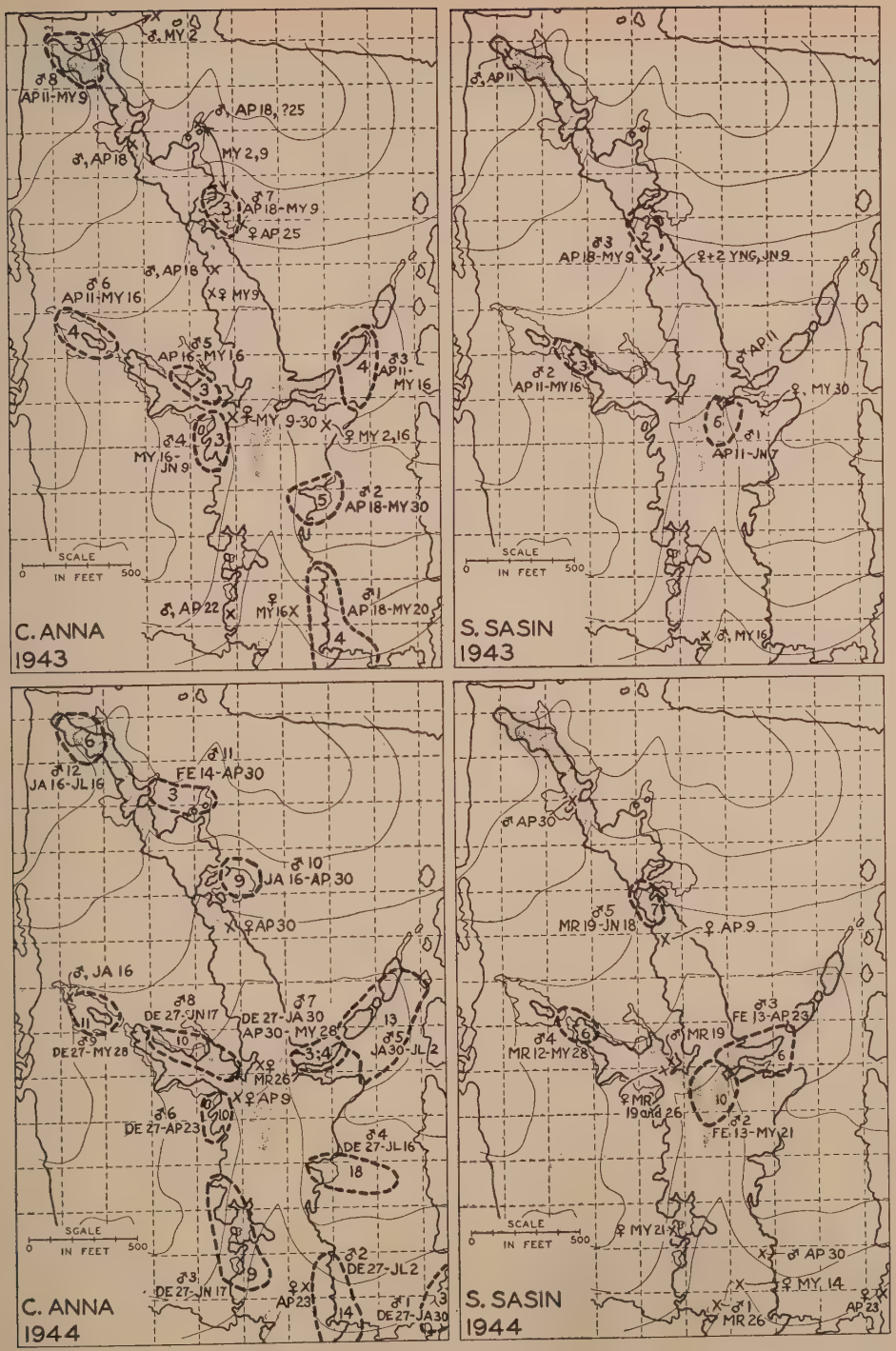

FIG. 5. Distribution of territorial males of the Anna (*C. anna*) and Allen (*S. sasin*) hummingbirds in the breeding seasons of 1943 and 1944. Enlarged core areas held by *C. anna* (see text) and territories of *S. sasin* are inclosed by heavy broken line. The figure within the broken line indicates number of separate days a male was observed on the area in the period given just outside the broken line. Territorial males are numbered. Occurrences of females and other males are each indicated by an X with accompanying date.

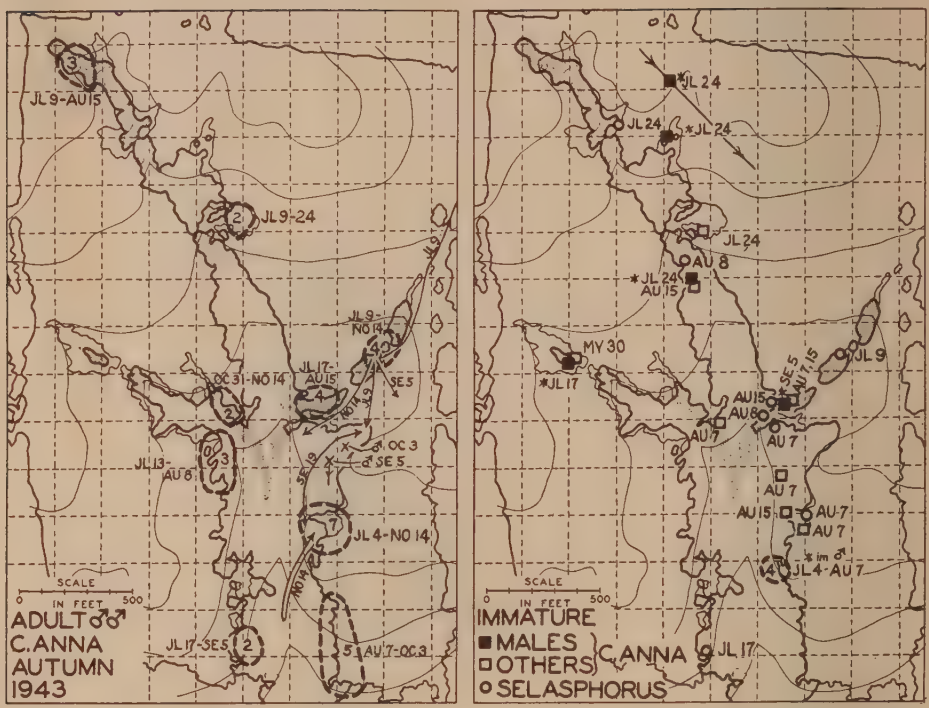

FIG. 6. Left, occurrence of adult territorial males of *Calypte anna,* autumn, 1943. Isolated occurrences of adult males indicated by X (see text). Certain flights of two adult territorial males indicated by long arrows; if axis of arrow continues beyond point, the end of the flight was not observed.

Right, occurrence of immature males of *C. anna* (singing at time of observation, denoted by asterisk), of other, additional individuals of *C. anna,* and of *Selasphorus* hummingbirds, the last probably comprised mainly of immature individuals of *S. sasin.* An immature male of *C. anna* was present on one area on four separate dates, as indicated.

conclusions predicated on assumptions concerning identity of individuals however strong the suggestion that in most cases the same individual occupied a given site in one breeding season.

SUMMARY OF DATA

1943

C. anna.—Eight resident males were present (Fig. 5). Two additional males may have been resident: One was recorded near the west end of the canyon on April 22 in an area occupied in other years and not closely adjacent to other areas occupied in 1943; an established male was noted on the same site later in the summer (Fig. 5). The second was a male noted in Upper Draw on April 18 and presumably also on the 25th; on May 2 and 9, male 7 flew to Upper Draw and back, and Upper Draw was otherwise unoccupied. On May 2 an extra unsettled male was present along the east border.

Females were recorded eight times: At one site, on May 2 and 16, at another on May 9, 16, and 30. But the other records are isolated occurrences, two of them in nesting habitat.

S. sasin.—Four resident males were present (Fig. 5). Only three are numbered in Figure 5. The male at the lower end of the canyon, on a steep area adjacent to private property and not checked easily, is considered a fourth because an established male was found here at least once each of the five years. A possible fifth resident male occurred at the upper end of the canyon on April 11; a sixth occurred on April 11 in the lower part of South Draw, a site occupied by *sasin* in other years.

Females were recorded twice: one with two fledglings on June 9, the other on May 30 in an area where nesting occurred in other years.

Contacts.—Male 3 of *S. sasin* (S3) and male

6 of *C. anna* (A6) were observed in aggressive and retaliatory chases on April 11 and 18. Clashes were noted on April 11 between A8 and an established, displaying male *sasin* not recorded subsequently. No clashes were observed on April 11 between A3 and the neighboring male *sasin,* whose area, however, was not occupied subsequently, whereas S1 remained at least through June 7. No clashes were observed between A7 and S3, or between males on these sites in any subsequent years as tall trees to the south of the main territory of *sasin* shielded it from that of *anna,* which latter was also upslope.

1944

C. anna.—Eleven resident males were present (numbers 2–11, Fig. 5). Male 1 was present only in the early part of the breeding season, in an area of eucalyptus trees not typical as male breeding territory and not occupied any other time in the five years. One of the eleven occupied sites was vacated between January 30 and April 30 (male 7). Active territorial competition between two males occurred on the site of male 9 on January 16.

Four isolated occurrences of females were recorded, March 26–April 30, all in typical nesting habitat.

S. sasin.—Five resident males were recorded (Fig. 5). Excluded are two displaying males observed only on April 30 in sites which, while seemingly suitable for *sasin,* were found unoccupied in all remaining observations. Also excluded is a male observed on March 19 at the lower end of North Draw displaying before a female with nesting material in her bill. The circumstance of three established males in adjacent areas and other observations suggest that this male may have been one of the three more likely than an additional male even though the site was occupied in other years. See further comment under "contacts."

Three isolated occurrences of females were recorded April 9–May 21, one of these being from an area where nesting occurred in other years. In addition, at one location on March 19 and 26 and at another on May 14, females were observed in typical nesting habitat.

Contacts.—S3 was present in an area previously and subsequently occupied by a male *anna* (A7). Announcement flights of S3 on March 19 and 26 toward the south border of its territory were evidently addressed to A5. No clashes were observed between A10 and S5. An aggressive chase of S4 toward A9 occurred on April 2. The displaying male *sasin* of March 19, mentioned above, was chased away by a male *anna,* presumably A8, and was not observed to return to the site.

1945

C. anna.—Ten resident males were present (Fig. 7). A possible eleventh was one observed April 13 near the lower end of the canyon. Adult males singing within oak-laurel forest on July 15 (two records) may represent earlier occupants of nearby territories in period of summer subsidence of territorial activity. An additional male on territory of male 2 on June 3 was engaged in challenge displays and chases with the latter. On July 16 no adult male was present here, but the area was held by an immature male.

Females were recorded four times, April 1–May 6, two of them from one site.

S. sasin.—Six resident males were present (Fig. 7). A possible seventh residency occurred at the lower end of North Draw, where a displaying male was present on April 22, and where a male, though not displaying or holding a post, was observed on April 1 and June 3.

Two isolated occurrences of females were recorded, April 1 and July 15, both in typical nesting habitat. In addition, one nesting territory of a female was found on May 6; on June 3 the nest contained two young almost ready to leave.

Contacts.—The overlap in territories A3 and A4 refers to a shift apparently related to the departure of S3. On April 1, 13, and 22, A4 presided over the center willow area along South Draw, with a patrol flight westward on April 13 to a shrub in the open area between the willows and the oak-laurel forest. On May 6 and 20, when S3 was absent, A4 (or at least another adult male *anna*) was present in the lower willow area, flying to and back from the center willow area on May 20. On this day, another adult male was present on the upper willow area. Subsequently a male was present on the lower area on May 27 and June 3 (records lumped under A3) and on June 3 a second was present on the middle willow area. Thus, whereas a male *sasin* and male *anna* were present along South Draw in April, after the departure of the former, two males of *anna* were present.

On April 15 and May 6, S6 presided over a willow area usually included in the territory of a male *anna.* A10 was present to the south of S6's territory on these days. Once A10 flew over S6's area on April 15 and the latter chased A10 for a distance of at least 40 feet, toward the main post occupied by A10. On April 15 and May 6, both birds displayed in easy hearing distance of each other. On May 27, S6 was absent and A10 held a post on the area previously occupied by S6. A10 also flew to perches to the south where he was more active on earlier dates. Also on May 27, a male *sasin* was established below the main area of terri-

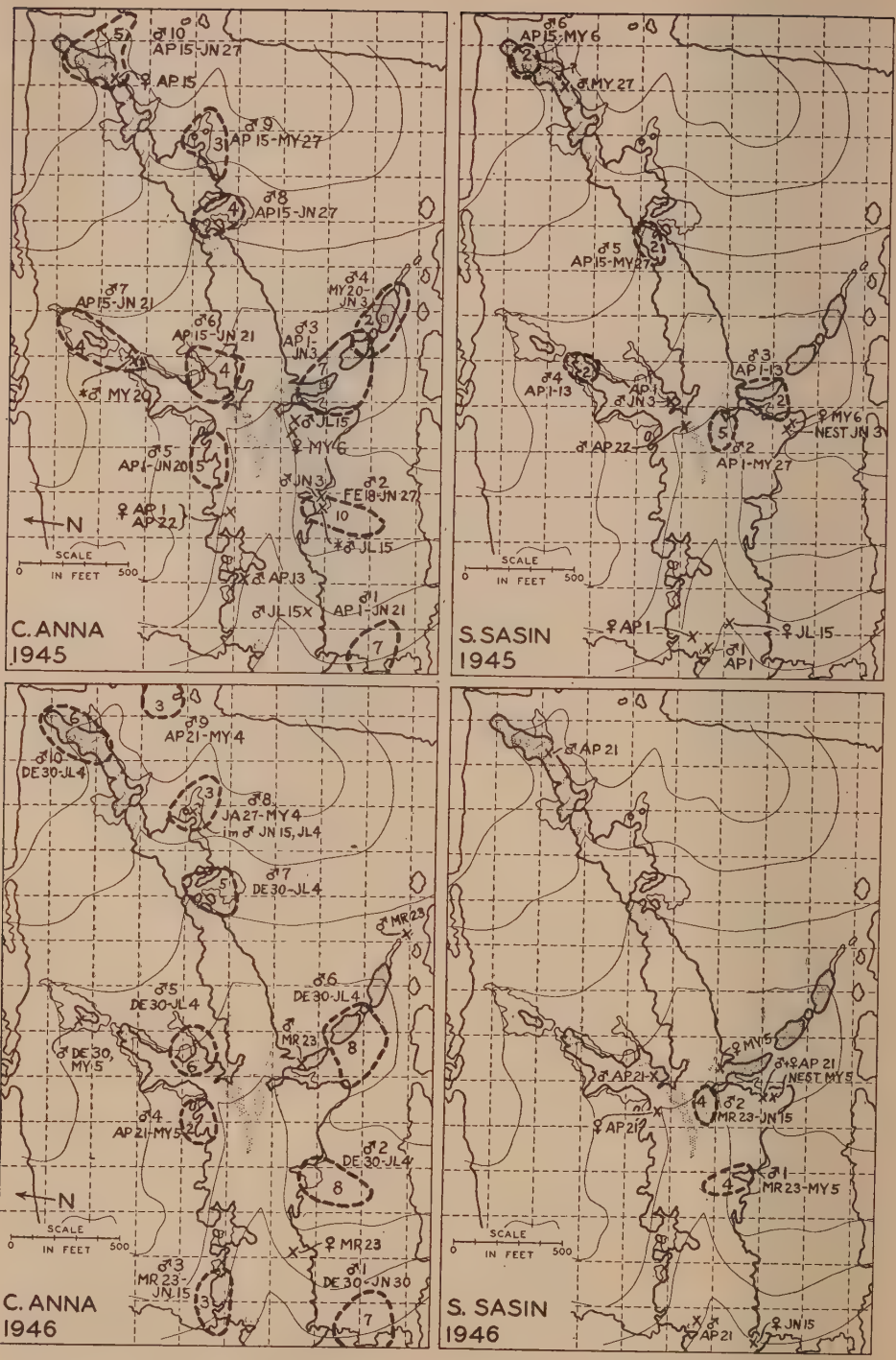

FIG. 7. Distribution of territorial males of *C. anna* and *S. sasin* in the breeding seasons of 1945 and 1946. See legend, Figure 5, for explanation.

torial activity of A10. The former occupied a prominent post, performed announcement flights, but did not display. Once A10 chased the male *sasin* westward for a distance of about 500 feet, A10 returning to his chief post promptly, the male *sasin* appearing at his three minutes later.

Along North Draw, territories of A7 and S4 were exclusive until after S4 left. On May 20, there was an immature male *anna* established on the area formerly occupied by S4, and on June 20, but not earlier, A7 included this area in his territory and sang on it.

Territories of A8 and S5 overlapped, though no clashes or chases were observed. Two males of the respective species were present here on April 15 and May 27; on May 4 A8 flew from his usual post into the willow area and on this date a male *sasin* was not located.

At the lower end of North Draw, the territory of A6 overlapped that of a possible seventh resident male *sasin*.

1946

C. anna.—Ten resident males were present (Fig. 7). A possible eleventh resident male in North Draw was seen only on December 30, 1945. On May 5, the adult male observed here performed announcement and exploring flights suggesting a newly arrived individual. A possible twelfth resident male was that seen in lower South Draw on March 23, in an area of *sasin* habitat not occupied this year. A singing male present in the upper part of South Draw on March 23 occurred in an area at no time used as a territory by this species. The area of male 8 was occupied by an immature male on June 15 and July 4.

But one female was recorded (March 23).

S. sasin.—Three resident males were present (that at lower end of canyon being unnumbered; see comments under 1943) (Fig. 7). A possible fourth was present at the lower end of North Draw, and a possible fifth at the upper end of the canyon, both on April 21. The male present to the south of the area of S2 on April 21 was probably S2 as no male was present on his territory on that date.

Three isolated occurrences of females were recorded, April 21–June 15. In addition, a female was present to the south of the territory of male 2 of April 21 and a male displayed before her. On May 5, a nest with one egg was found here.

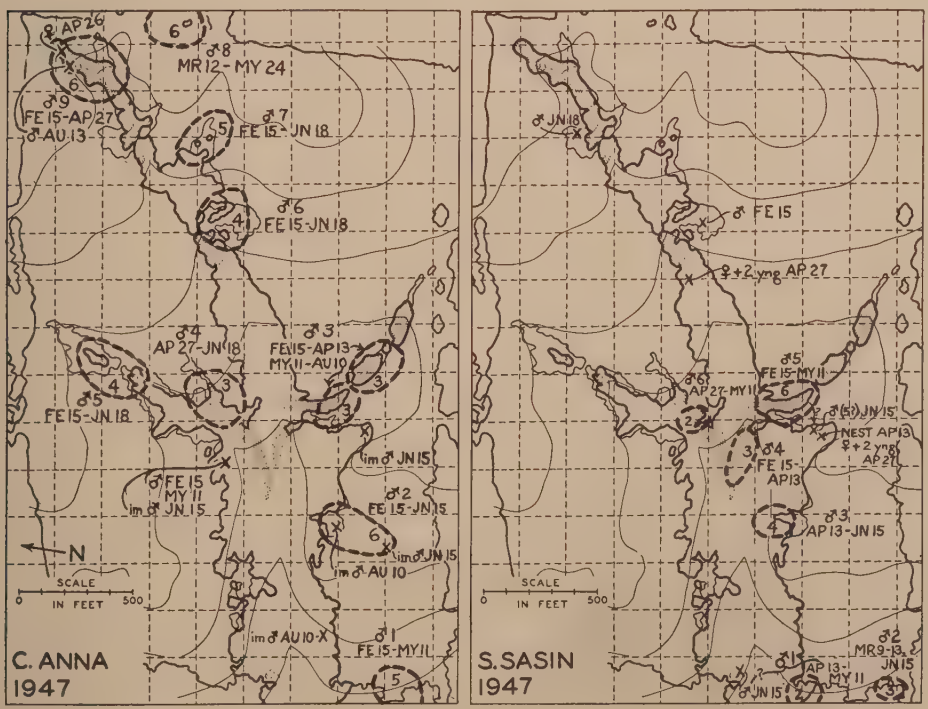

FIG. 8. Distribution of territorial males of *C. anna* and *S. sasin* in the breeding season of 1947. See legend, Figure 5, for explanation.

Contacts.—On April 21, two males of *sasin* were observed in areas included in the territories of males of *anna* (A5 and A10). Territories of A2 and S1 overlapped slightly; posts of these respective males were no more than 50 feet apart but on four different days when both were present, no clashes were observed. This was so, evidently, because A2 guarded the open, brush-covered west-facing slope to the south of its main post, whereas S1 guarded a small area of soft chaparral on a steep north-facing slope. The main post of S1 was on the north side of an oak, away from the area guarded by A2.

1947

C. anna.—Nine resident males were present (Fig. 8). A possible tenth may be represented by males observed at the lower end of North Draw on February 15 and May 11, in an area occupied in all previous years. On this area an immature male was established on June 15. Two other established immature males were observed on June 15, one within the territory of A2. An immature male was observed settled and alone on the latter territory on August 10.

One female, the only one for the season, was observed gathering nesting material in the territory of A6 on April 26.

S. sasin.—Six resident males were present (Fig. 8). A male observed on February 15 below Upper Draw was not holding a post. Other occurrences of males are June 18 (at upper end), June 15 (near South Draw), June 15 (at southwest corner), and June 15 (near lower end on south-facing slope). Only the last of these was established and displaying, and it may represent a seventh possible resident.

Two nesting females were recorded: the first with two fledglings on April 27 and the second with a nest (two nestlings about a week old) on April 13 and two fledglings on April 27.

Contacts.—No male of *sasin* was present in North Draw; on two of the four days when A4 was observed, his chief post was in the area occupied by *sasin* in other years, and on the remaining two days, his perch was higher up in the draw. Overlap occurred between territories of A4 and S6, but no reactions were observed, in part presumably because the favored area of S6 was separated from that of A4 by a mass of high shrubs on a slope, S6 being at the lower side of this. No reactions were observed between closely neighboring males A2 and S3, A1 and S1, and A1 and S2. In the second and third of these, vegetational walls separated the main, more restricted areas of activity of the *sasin* males from that of A1. A shift in the territory of A3 indicated in Figure 8 was first evident when, on May 11, A3 used a post at the upper end of the lower willow area of South Draw while S5 perched at least 100 feet below and to the north. On June 15, when a male *sasin* was no longer present, and also on August 18, a male *anna* was present in the lower willow area and adjacent forest border. The latter was the only adult male found in South Draw on these dates.

Discussion of Results

The evidence clearly points to a dynamic interaction between breeding populations of *C. anna* and *S. sasin.* Unlike most other described examples of interspecific competition in birds, this one involves differences in habitat selection of the sexes of the competing species. Lack (1949, p. 301), enumerating possible outcomes of competition between closely related species, states that in observed cases such species may (1) replace each other geographically, (2) replace each other ecologically, or (3) take different foods in the same habitat. Under the second of these outcomes, we must recognize two categories: (a) those species in which pairs occupy a given habitat, and (b) those species in which the sexes occupy different habitats. Among North American hummingbirds, pairs occupy the same habitat in *Calypte costae* at least (personal observations; see also Grinnell and Miller 1944, p. 218). In *Calypte anna* and *Selasphorus sasin* the sexes occupy different habitats, as is also true in *Archilochus alexandri* and *Stellula calliope* (Grinnell and Miller 1944, pp. 217, 225), *Archilochus colubris* (Johnston 1947, p. 51), and possibly *Selasphorus platycercus* (Hering 1948, p. 53).

As between *anna* and *sasin,* the breeding-season habitats of the two sexes differ more in the former than in the latter. This would suggest greater overlap in activities of the two sexes in *sasin* than in *anna,* and this is borne out by the greater frequency of nesting observations for *sasin* than for *anna* in Woolsey Canyon (see summary of data). As for *anna,* my failure to find nests or fledglings in Woolsey Canyon in the five-year period and the paucity of records of females for that area convinces me that but few nestings occurred in the canyon. Each site where

a female was observed two or three times in successive weeks represented typical nesting habitat (see maps for 1943 and 1945, Figs. 5 and 7). In these instances and one other (see map for 1947, Fig. 8), certain features of behavior suggested that the females were locally resident individuals. Thus, the records reveal three or four possible nestings in the five-year period, no more. I feel justified in stressing this because even though no systematic search for nests was conducted, locally settled hummingbirds are usually easy to detect in a familiar area of census work. Some females were probably overlooked, but not so many, I am certain, as to negate the recorded disparity in local representation of the two sexes. Thus, in the breeding populations of both *anna* and *sasin* in Woolsey Canyon, considering the breeding season as a whole rather than any given day or part of the season, males were more numerous than females, and this disparity was more marked in *anna* than in *sasin*.

The observations from Woolsey Canyon offer no more than this on interspecific strife in females. For the males, however, data summarized earlier reveal several important points. First, neighboring males of the two species may compete territorially through aggressive displays, challenges, and chases. When such reactions between neighboring males have not been observed, it has been possible in almost all instances to recognize masses of screening vegetation which served to separate somewhat the areas guarded and thus to keep the males apart (but see beyond). Adult males of *sasin* observed on certain sites only once in a season could have failed to establish themselves because established males of *anna* displaced them. The many observations of aggression and of use of *sasin* habitat by *anna* all strongly suggest that an *anna* male may effectively prevent a *sasin* male from occupying a territory.

We can get at this matter directly by summarizing data on occupation of various territorial sites of the two species for the five-year period. This is done in Figure 10. For each site, the number of seasons it was occupied is given. For *anna*, twelve sites presumably could have been occupied each year with a potential total of 12 × 5 or 60 male residents over the five years. Actually there were 48, or 80 per cent of the potential total. For *sasin*, ten sites provided a potential total of 50 male residents; actually there were 24 or 48 per cent of the potential total. If we include doubtful residencies (Table II), these percentages are 90 and 60, respectively. Another way of bringing this difference out is to say that nine of twelve *anna* sites were occupied four or five years, whereas only two of the ten *sasin* sites were occupied four or five years.

TABLE II. *Summation of breeding-season records of adult male hummingbirds in Woolsey Canyon*

	Selasphorus sasin		*Calypte anna*	
	Residents	Others*	Residents	Others*
1943	4 + 2?		8 + 2?	1
1944	5	3	11	2
1945	6 + 1?	2?	10 + 1?	
1946	3 + 2?		10 + 2?	1
1947	6 + 1?		9 + 1?	
	24	6 | 5	48	6 | 3
		11		9

* Single observations of birds whose behavior did not suggest that they might be residents.

The percentage for *sasin* falls to 45 or 40 per cent when we recognize that along South Draw, there were one or two additional sites suitable for, but never found occupied by, *sasin* (Fig. 10). The two willow areas were similar to other willow areas occupied in the Berkeley Hills, and at least the middle one of the three areas appeared as suitable for *sasin* as the lower (northern) one. Along South Draw a male *anna* was present each year; moreover several prominent perches available to the *anna* male in this narrow belt of vegetation provided effective vistas of the entire slope, thus contributing to his efficiency in meeting intruders. I conclude

from comparisons of situations occupied by *sasin* males that South Draw offered habitat which would have been occupied by *sasin* in the absence of *anna*. It is my clear impression that this habitat was more favorable for *sasin* than the two other queried sites shown in Figure 10. At each of the latter sites, where a male was observed only on one day in the five-year period, the areas of soft-foliaged shrubs were more inclosed by neighboring trees than any of the other areas used by *sasin*, and this is evidently a factor figuring in the selection of sites.

Only two instances of apparent displacement of *anna* by *sasin* were noted in Woolsey Canyon, S3 in 1944 and S6 in 1945. A third example was recorded in 1944 near the study area: An *anna* male which guarded a willow area on January 16, 31, and February 27, was replaced by a *sasin* male found six times and on each visit between March 19 and May 21. During this latter period but not earlier, an *anna* male was present about 400 feet upslope from the *sasin* male through April 9; subsequently a male was present at another post about 300 feet below the site of the *sasin* male at least through May 28.

While factors other than competition with *anna* no doubt effect the density of *sasin* males, I interpret the data from Woolsey Canyon to indicate that the density of *anna* operated to lower the density of *sasin* below levels which the area could support in the absence of *anna*. It is striking, first of all, that the two sites occupied by *sasin* four and five years were sites unattractive, as it were, to *anna*. Site E (*sasin*) was in a well-wooded, rather deep part of the canyon with dense, rank undergrowth surrounding the willow areas. This situation falls out of the range of habitats normally selected by *anna* males. At site A (*sasin*), the willow area was within a well-wooded, steep south-facing slope, somewhat more open and drier than site E, but also atypical for *anna* males. All other *sasin* sites actually occupied were next to or part of *anna* sites. Between certain sites, local vegetation walls, already mentioned, were considered to reduce conflict between neighboring males; at least my failure to observe conflict under such circumstances seemed explainable in part by the reduced exposure of territorial posts of neighboring males to each other. While the local vegetation may reduce such conflict, it cannot eliminate it due to the normal amount of activity on wing and to the responsiveness of belligerent territorial males to flight sounds of other hummers near or on their domain. Thus, along the west border, *anna* site B overlapped *sasin* sites B and C, which, though they were partly sheltered by vegetation (see above), were each found to be occupied only one out of five years.

Records of resident males, supposed residents, and visitors for the five-year period are summarized in Table II. Single records of adult males in June and July are excluded from this table since by that time of the season their appearance would not influence critically the composition of the breeding population; indeed, some of these males had probably deserted breeding territories elsewhere. For the five-year period, the resident population of *sasin* averages 5 or 6 males, that of *anna*, 10 or 11 males.

Table II shows further that the proportion of uncertain residents and visitors to residents is greater in *sasin* (11:24) than in *anna* (9:48). Of the two species, *anna* is the more conspicuous; therefore, if error has occurred, it is that not all the visitant or potential resident individuals of *sasin* were detected and that the actual difference was probably greater than indicated by my figures. Migrants are not considered to figure importantly in this difference. The usual appearance of *sasin* in the San Francisco Bay region in early February and its breeding restriction to the humid coast belt northward only to the southwestern corner of Oregon indicate that within the northern sector of this range, it probably arrives no later than late February. This is supported by reports on *Selasphorus rufus*

from coastal Oregon, where this species arrives in late February and early March (Gabrielson and Jewett 1940, p. 364), as in the San Francisco Bay region. In other words, the mass of the population of *sasin* is considered to arrive on its breeding grounds in advance of that part of the breeding season including most of the records of visitors and doubtful residents of the Woolsey Canyon population here discussed. Granting this, the difference in proportions between the totals given in Table II may also be taken to reflect the depressing effect of *anna* on *sasin* in such areas as Woolsey Canyon. Were the proportion of doubtful residents and visitors in *anna* comparable to that in *sasin*, the total would be at least twice that recorded in Table II. Moreover, the proportion of visitors and doubtful residents to residents in *sasin*, in the light of arguments presented, indicates that available sites for residency are likely, if not almost certain, to be taken up by mid-April.

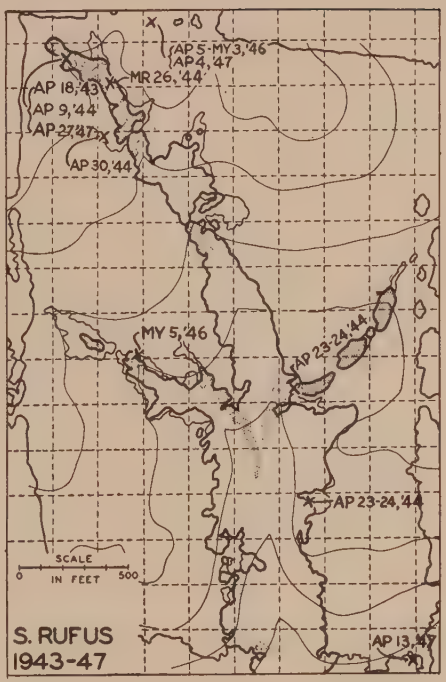

Fig. 9. Occurrences of adult males of the rufous hummingbird (*Selasphorus rufus*), most of them territorially established (see text), in the breeding seasons of 1943–1947. *S. rufus* is not known to breed here, however.

Occurrence of Other Species of Hummingbirds

Two other species occur as migrants in the San Francisco Bay region. The calliope hummingbird (*Stellula calliope*) is present from late March to mid-May. Fall occurrence need not concern us here (Grinnell and Miller 1944). In Woolsey Canyon the calliope hummingbird was observed only a few times in the month of April. Males perform territorial flight-displays on feeding areas, but these are usually held only briefly. The numbers present are small and the most frequent occurrences are in garden areas and eucalyptus groves, that is, in areas essentially removed from those where competition between territorial males of the breeding species occurs.

This, however, is not true of the second species of migrant, the rufous hummingbird (*Selasphorus rufus*), which occurs from late February to mid-May. Certain males of this species take up territorial stations, perform flight displays, and evidently may hold these stations for periods of a few days to several weeks. At least it is true that a given site is found to be occupied on successive dates. I have five such records: April 4–22, April 5–May 3, April 9–23, April 23–24 (2 records). Three of these were obtained in Woolsey Canyon (Fig. 9). Yet there is no evidence that *rufus* breeds south of Oregon. *Sasin* breeds northward only along the coast of California and probably in the southwestern corner of Oregon (Gabrielson and Jewett 1940, p. 364). The distributional limits of the two species are not known to approach each other so closely that even sporadic interbreeding may be suspected to occur.

As suggested by Figure 9, *rufus* males occur in situations used by *sasin*, but also in upland areas away from riparian thickets. *Rufus* may thus meet competitively

both *sasin* and *anna*. A summary of observations follows:

Site D of *sasin* (Fig. 10), occupied by *sasin* in 1946 and 1947, was used by *rufus* in 1944, even to the identical look-out post. Here challenge and retaliatory flights between the *rufus* male and *anna* male 4 (Fig. 5) were observed.

Site J of *sasin* was occupied by that species in 1945 (Fig. 7). In 1943, a *sasin* male occurred there on April 11, but was not found on April 18, when a *rufus* male was present. There was no confusion of identity here, as these birds performed flight displays, which are distinctive. In 1944, a *rufus* male was present on March 26 and on April 9. In 1946, a *sasin* male was present on April 21. In 1947 *rufus* was present on April 27, but *sasin* was not recorded there.

On site C of *sasin*, in 1947, a *rufus* male was present on April 13, but a *sasin* male was present before and after, as indicated in Figure 6.

On site F of *sasin*, in 1944, a *rufus* male was present on April 23 and 24. Site F was occupied by *sasin* that year (Fig. 4). On April 23, the *rufus* male was chased by *anna* from the south. No male of *sasin* was present in the willow thicket on that date, but one was found along the edge of the oak woodland above and to the west of the willow thicket. It remained here throughout the period of observation; moreover, on March 19, the *sasin* male present in the willow thicket used the same part of the woodland edge, flying here from his main post atop the thicket. It therefore seems likely that the *sasin* male observed on April 23 was the one earlier occupying site F. It is of interest that on April 30, neither *rufus* nor *sasin* was present on site F, but an *anna* male was established then and later (Fig. 5).

On *anna* site L (Fig. 10), a *rufus* male occurred in 1946 and 1947 (Fig. 9). An *anna* male was present in each of those two years (Figs. 7, 8), but no contacts between it and the *rufus* male were observed. The site occupied by the *rufus* male was to the north of the main post of the *anna* male, but more importantly, it was located in an area with scattered eucalyptus trees and small shrubs within which the *rufus* male confined his activity. The male of *rufus* displays a restricted territoriality like that of *sasin*. Here the *rufus* male was active in and above a rather sheltered shrub area, whereas

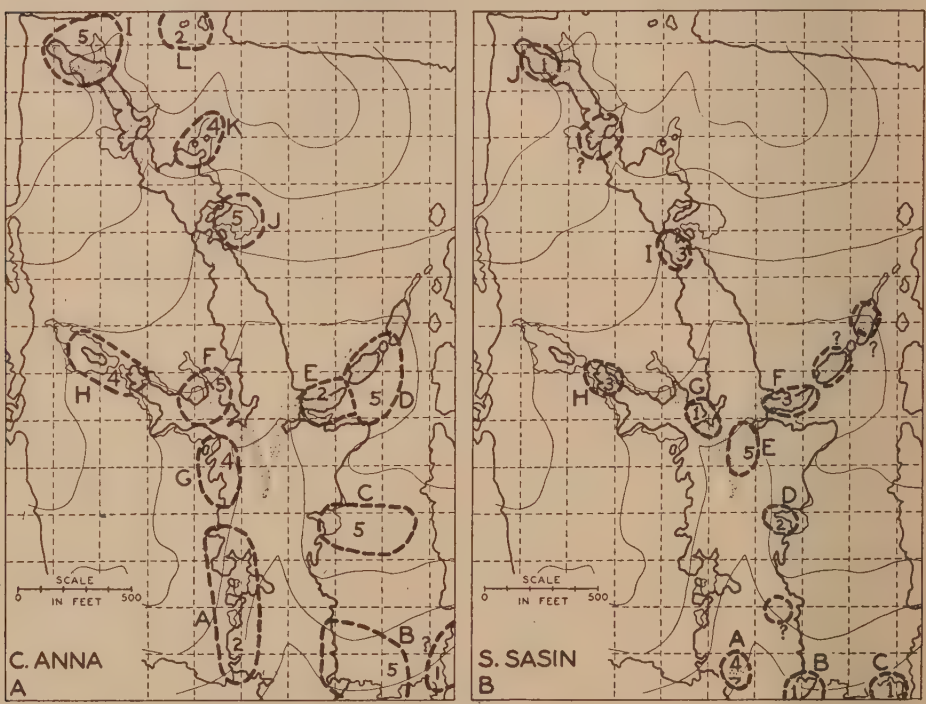

FIG. 10. Areas occupied by territorial males of *Calypte anna* (A) and *Selasphorus sasin* (B) in the period of 1943–1947. Within the heavy broken line bounding each area, a figure indicates the number of breeding seasons the area was occupied.

the *anna* male was interested in the edge of this vegetation and other islands of shrubs and trees in a more open part of the area and adjacent to a grassy flat to the west.

Other occurrences of *rufus* shown in Figure 9 were those of males present only briefly after detection.

Several points of significance may now be summarized. Records from Woolsey Canyon together with other observations near the study area indicate that for *rufus* males the ecological range of vegetational substratum suitable or acceptable for territories is greater than for *sasin* males, at least in the Berkeley Hills. Males of *rufus* arrive a few weeks later than those of *sasin* and are not present in maximal numbers until late March and April. However, not all breeding males of *sasin* are settled on territories by late February. Numbers of *sasin* males continue to rise through March, and as *rufus* is a common migrant, contacts between *rufus* and potential or actual breeding males of *sasin* possibly occur with significant frequency. I have no direct observations from Woolsey Canyon of aggression or conflict between males of *sasin* and *rufus,* but other observations indicate, as do the occurrences of *rufus* already described, that such contacts must occur. Their frequency is certainly greater than suggested by the records here summarized, for weekly or biweekly visits to the study area, though adequate to obtain estimates on populations of residents, were too infrequent to record more than a fraction of the visits of males of *S. rufus.* Thus, the evidence points to the presence of *rufus* males as a factor limiting the success of establishment and maintenance of territories by *sasin.*

Factors Affecting Competition

Both direct and indirect reference has been made to a number of factors affecting competition. Given the facts of overlap in habitat distribution, correlated similarity in structure and feeding habits, and consequent competition, we may attempt to identify those which can or do influence the outcome of competition, at least under the conditions prevailing in Woolsey Canyon.

The difference in breeding seasons of the two species is perhaps the most important factor. Breeding begins sooner in *anna,* and male territories are occupied in this permanently resident species well in advance of the time that males of *sasin* arrive. There is first, then, the fact of an early start in nesting of *anna.* Second, males of *anna,* once established, become familiar with their domain and alert to intrusions. The behavior of adult males often quickly reveals whether they are local residents or just transients or local pioneers (Pitelka, MS). Thus, the advantage of mere prior presence is reinforced by a psychological advantage which a territorial male has. Third, the persistent singing of breeding males in *anna* announces presence to other males of either species, and this may well discourage *sasin* males from exploring or even entering occupied *anna* territories. Fourth, the examination of morphological characters showed that *anna* is a larger species with a more highly evolved head iridescence which enhances the flash effect in its flight display.

The fact of size differences in the territorial spheres of males of the two species is more difficult to evaluate with respect to competition. *Anna* defends a larger, ecologically more varied space than *sasin,* and associated with this difference is the more complex territorial behavior of *anna.* With the advantages enumerated in the previous paragraph, an *anna* male may effectively exclude from a part of its territory attractive to *sasin* a potential resident of the latter species. But it is at this point that the ensuing events may favor *sasin.* If *sasin* becomes established, the resulting comparatively restricted territory of *sasin,* usually peripheral to the main area of activity of *anna,* is given up by the latter. Occasionally, however, *sasin* may actually displace an established male of *anna* (three cases discussed above). The details of success in com-

petitive establishment of *sasin* males in these instances are unknown, and the circumstances, probably different in each instance, may be affected by various factors, among them the following: distraction of *anna* males in intraspecific competition; individual variation in belligerence and the outcome of initial contacts between competing males; and occurrence of special features of vegetational spacing which may reduce competition early in an occupation by *sasin*.

No actual or potential advantage in any feature of behavior or ecology can be recognized for *sasin* in its competition with *anna*. As already shown, *sasin* occupied most regularly those sites which were out of the range of habitat conditions selected by *anna*. In those three known situations where *sasin* displaced *anna*, I am unable to detect any common habitat factors that would suggest why *sasin* should have been successful in these instances and not in others. The important fact remains that *sasin* can be successful in competition with *anna*. Finally, evidence on local occurrence of a congener of *sasin*, the migrant species *rufus*, indicates that the latter complicates the interrelations of *anna* and *sasin*. Presence of *rufus* may be a factor at least occasionally operating to reduce density of resident males of *sasin*.

The early territoriality of immature males of *anna* evidently does not influence critically the densities of resident hummingbirds, as by mid-May, when the first assertive immature males appear, the breeding season for both species is in its last quarter.

Few reasonably clear examples of depressive influence on populations as a result of interspecific competition in natural populations of birds are known (Errington 1946, p. 171). One of the best is that of the native bob-white (*Colinus virginianus*) and the introduced pheasant (*Phasianus colchicus*) in Iowa (Errington 1945). In the competition between *Calypte anna* and *Selasphorus sasin*, we apparently have a mutual, but not balanced depression of population densities. In the Berkeley Hills, this interaction favors *anna*. Does it favor *sasin* anywhere in the area where breeding distributions overlap? From observations in various parts of coastal California, I am inclined to think that in the overlap area in the southern half of the narrow coastal breeding range of *sasin*, this species is favored only to the extent that *anna* is removed as a competitor by unfavorable habitat conditions, as in more or less forested canyons near the coast. In *anna*, at the outermost margin of its range, sparseness of territorial males may be an unfavorable factor, as territorial belligerence is of course aggravated by proximity of other males. But otherwise, considering the equipment of *anna* as a species, and given habitat conditions favorable to *anna* and *sasin*, the former will evidently be the more successful.

Summary and Conclusions

Ecological data on two species of western American hummingbirds, *Calypte anna* and *Selasphorus sasin*, were derived from a five-year population study of breeding birds on a 125-acre canyon area in the Berkeley Hills, on the east shore of San Francisco Bay, California. From morphological comparisons and a summary of extensive observations on territoriality and habitat distribution, factors which influence the interrelations of these two species are identified.

On the study area, the breeding population averaged 5–6 males of *sasin* and 10–11 males of *anna*. For females, which enter a pair-bond only to mate and breed in habitats different from those of their respective males, numbers on the study area were much lower than for males.

The habitats of males of the two species overlap to the extent that territories occupied by *sasin*, usually areas of willows, are often peripheral to or included in the upland territories of *anna;* and in these areas of overlap competition occurs.

In general, territorial sites suitable for each species were used in a number of

successive years; and from the number of breeding seasons in which these sites were occupied, a relative measure of actual versus potential density was obtained. The resulting figures show that a mutual, but unbalanced depression of population levels of at least males occurred. In this interaction, *Calypte anna* was favored. Over the five years and excluding doubtful residents, 80 per cent occupation of suitable sites occurred in *anna,* only 48 per cent and probably less in *sasin.* But three instances of apparent displacement of *anna* by *sasin* were recorded.

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COMPARISON OF SPRING DIATOM CROPS OF WESTERN LAKE ERIE IN 1949 AND 1950

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INTRODUCTION

During the spring months of 1949 and 1950 the diatom crops arising in western Lake Erie were studied intensively in attempts to determine and compare the approximate quantities of diatoms represented and the rates of population growth and decay.

A mobile sampling method, previously described (Verduin 1951a), was employed during both years. Water samples were drawn every half hour while cruising at about 10 mi. per hr. and the diatoms were removed with No. 25 silk bolting cloth filters for counting. Volumetric units were used in counting (Welch 1948, p. 292). A technique described by Olson (1950) facilitated counting of filamentous forms. Samples were counted within a day of the time they were collected and were observed in fresh (unformalinized) condition.

Samples collected from a moving boat represent water from near the surface but they are not strictly surface samples since the surface water is broken and pushed aside by the bow-wave. This fact is emphasized during the summer when blue-green communities are concentrated in the surface layer. If speed is reduced and the boat is nosed gently into such a community, true surface samples yield phenomenal population densities of *Anabaena* and *Microcystis* but samples caught from the side of the boat while cruising through such a community yield only small populations.

This method of sampling eliminates designation of stations and no attempts are made to reoccupy the same sampling locations on successive sampling trips. Instead, a circuit is mapped out and samples are drawn at uniform intervals on that circuit. After the samples have been studied the number of different communities encountered on a trip can be determined by noting population densities and species composition. If a single community occupies a fairly large area (fifteen miles across or more) the chances of encountering that community on successive sampling dates are good. Such conditions are found in western Lake Erie in the spring months. During the summer and fall months, however, the communities do not occupy such large areas or attain the high population densities observed in spring, and attempts to identify a given community on successive sampling trips have not yet been successful during those seasons.

In estimating the quantity of diatoms contained in a crop, the sampling date showing the highest population density was used and all samples showing the species composition of that community were combined to yield the average population density. The area occupied was estimated by mapping the sampling route and noting the times when the community was encountered and when it was left behind, thus approximating the linear dimensions of the community. Since surface samples are fairly representative of the vertical water column in western Lake Erie (Chandler 1940) the average depth in the area, obtained from U. S. Lake Survey charts. was the only other statistic needed to provide an estimate of total diatom volume.

In studying growth and decay of populations, the three consecutive samples yielding the highest average crop were used to represent the population on a given date. In this way, samples well within the community boundary were obtained and the effects of mixing at the periphery

of the community would not influence the shape of the curves representing growth and decay.

The radiation data reported here were obtained from the continuous records of the Solar Radiation Station maintained at Put-In-Bay by the Stone Institute of Hydrobiology.

Ash-free dry weights of plankton and other suspended matter were obtained by igniting oven-dry samples in porcelain crucibles over a clean gas flame; suspended matter from turbid water was collected with a Foerst centrifuge.

Comparison of Yield in the 1949 and 1950 Spring Crops

The diatom community in the spring of 1949 was almost a pure stand (97%) of *Tabellaria fenestrata*, and it occupied an area of about 1,300 km.^{2}. The average standing crop (14 samples) at the time of maximum population density (April 12) was 16×10^9 μ^3 of diatoms per liter of water. In 1950, an *Asterionella-Cyclotella* community (about 50% each by volume) occupied an area of 274 km.^{2} and attained a population density (average of 4 samples, May 11) of about 6×10^9 μ^3 per liter. In Figure 1, a diagram is shown comparing these two communities. The average depth in the area is about 8 m. so the total diatom volume represented by the 1949 community amounted to about $(16 \times 10^9 \times 1{,}300 \times .008 \times 10^{12})$ 1.7×10^{23} μ^3 or 1.7×10^5 m.^{3} of diatoms. The ash-free dry-weight of these diatoms was about 3×10^{-10} mg. per μ^3. So the figure above represents 5×10^7 kg. of organic matter. The total diatom volume of the 1950 community amounted to about $(6 \times 10^9 \times 274 \times .008 \times 10^{12})$ 0.13×10^{23} μ^3

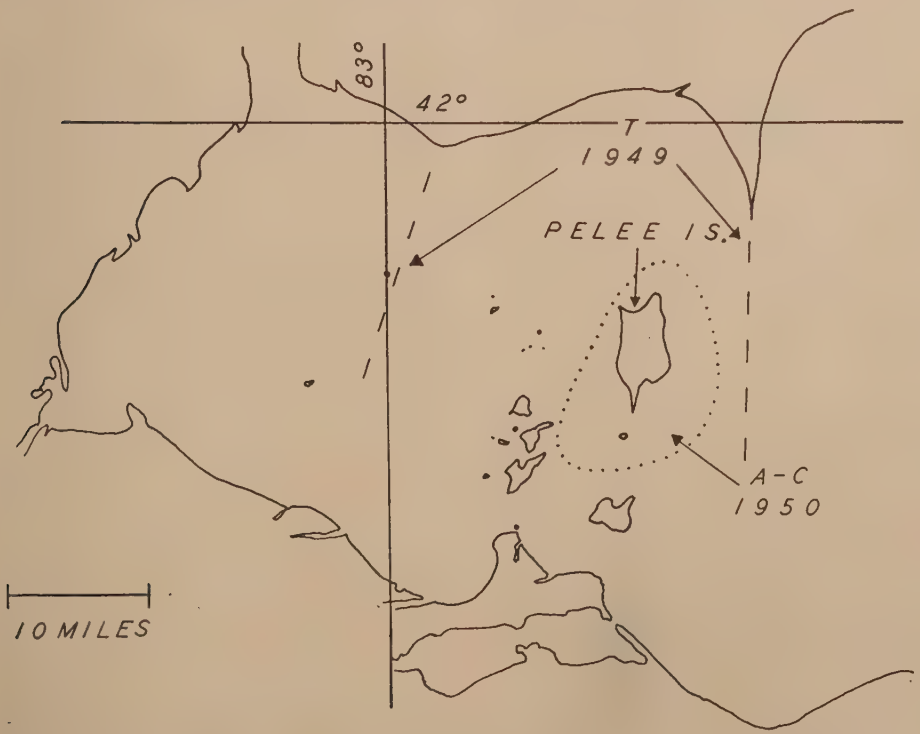

Fig. 1. Comparison of the size of the Tabellaria community (T) of 1949 with that of the *Asterionella-Cyclotella* community (A-C) of 1950.

or 0.13×10^5 m.^{3} of diatoms, representing some 0.4×10^7 kg. of organic matter. A comparison of the two years shows that the spring diatom crop of 1949 contributed 12 times as much organic matter as did the 1950 crop. The diatom yield of 1950 is best described as a "crop failure"!

The westward extent of the diatom communities each year was limited by the presence of turbid areas. The transition zone between clear and turbid water was never more than a few miles wide, and frequently the line between different water masses was so sharp it could be seen with the naked eye. In the distance the turbid water would then appear like a cloud shadow on the water, and when crossing the line it would be possible for a man with one bucket in each hand to sample clear and turbid water simultaneously. On April 12, 1949, in water west of the line (Fig. 1) 9 samples had an average turbidity of 25 ppm, while 9 samples east of the line had an average turbidity of 12 ppm. On May 11, 1950, 8 samples west of the line had an average turbidity of 27 ppm, while 4 samples within the enclosed area had an average turbidity of 15 ppm.

The significance of a turbidity of 12 ppm as compared to one of 25 ppm can be demonstrated by comparing the depth at which light intensity equals 1% of surface light in each case. For water having turbidity of 25 ppm this illuminated zone was 2.7 m. thick; for water having turbidity of 12 ppm the zone was 4.8 m. thick (cf. Chandler 1942). In the turbid water the illuminated zone represents about one-fourth of the water column, while in the clear water it represents one-half of it. Diatoms being carried up and down in the water column would, in clear water, spend about 6 hours out of 24 in the illuminated zone; in turbid water only 3 hours out of 24 are spent there. When one considers that respiration rates approximate 10% of maximal photosynthesis (Verduin 1951b) then the comparative growth-inhibiting influence of 25 ppm turbidity becomes obvious.

The diatom populations in the turbid water west of the lines attained less than one-sixth the density of the clear water populations. For the purpose of the present comparison these turbid-water populations have been neglected. The 1950 spring crop failure can be attributed primarily to the much greater extent of turbid water in western Lake Erie during 1950 as compared to 1949.

The eastward limit of the diatom communities was less clearly defined than the westward limit. In a transition zone having a width of about 10 mi. the communities found in the areas shown in Figure 1 changed to a community dominated by *Stephanodiscus niagarae* (turbidity in this region was 7 ppm). Lake Erie deepens rapidly eastward to a depth of about 18 m. The *Stephanodiscus* community is apparently representative of this deeper water, and has also been neglected in the comparison made above.

Comparison of Population Densities and Times of Occurrence

The time course of the 1949 diatom pulse is compared with that of 1950 in Figure 2. It is apparent that the 1950 pulse occurred about a month later than that of 1949, and its maximal density was only 40% of that observed in 1949.

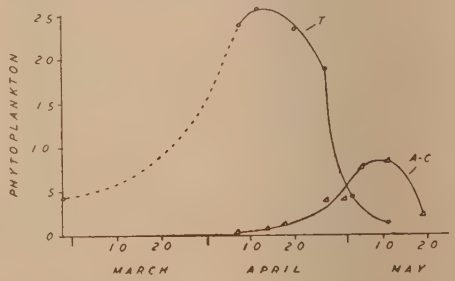

Fig. 2. Diatom populations (μ^3 per liter $\times 10^{-9}$) graphed against time. The curve labelled T represents the *Tabellaria* community of 1949, the A-C curve represents the *Asterionella-Cyclotella* community of 1950.

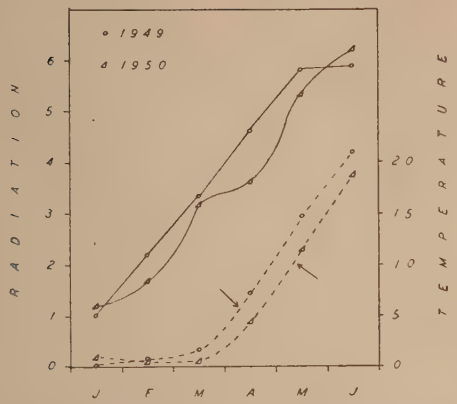

FIG. 3. Comparison of the radiation (solid lines, langleys per day $\times 10^{-2}$) and water temperature (broken lines, deg. C., monthly means of daily observations) curves for the first six months of 1949 and 1950.

The spring of 1949 was conspicuously warm and clear, while that of 1950 was characterized by cold, cloudy weather. The data on light and water temperature graphed in Figure 3 emphasize this contrast. It is interesting that in 1949 the diatom pulse reached its peak at a water temperature of about 6° C. (see arrows on temperature curves in Figure 3) while in 1950 the pulse reached its peak at a water temperature of about 10° C. It seems unlikely that retarded water temperatures delayed the 1950 pulse; the cloudy weather, with consequent restriction of the euphotic zone, was probably the major factor responsible for the delay.

The factors responsible for the low peak of the 1950 pulse were not determined. Analyses of dissolved materials were not made and it is possible that low concentrations of an essential element limited the diatom crop, but when the position of the 1950 pulse on the temperature curve is noted another possible explanation suggests itself: in 1950 growth may have been terminated by super-optimal water temperatures.

The fact that *Tabellaria* was the dominant diatom during 1949 while it was virtually absent in 1950 has not been explained. Occasional *Tabellaria* cells were observed in the 1950 samples so apparently an inoculum of these was present in 1950. The species of *Cyclotella* which was associated with *Asterionella* in 1950 had never before been observed as a major component in western Lake Erie communities. Dr. Ruth Patrick, of the Philadelphia Academy of Natural Sciences, identified it as *C. melosiroides*.

The exponential phase of the 1949 pulse was not sampled with adequate frequency and so no accurate growth rate can be calculated for 1949; but 6 datum points appear on the growth side of the 1950 curve and these points when graphed on a logarithmic ordinate, as in Figure 4, lie on a straight line. The growth rate indicated by the slope of the line amounts to a doubling of the population every 7 days. This rate represents only a single season's observations and that a conspicuously cloudy one. Future studies will show whether clearer seasons support higher growth rates.

Source of Turbidity in Western Lake Erie

Although the study described above was not designed to determine the source of turbidity, certain observations made dur-

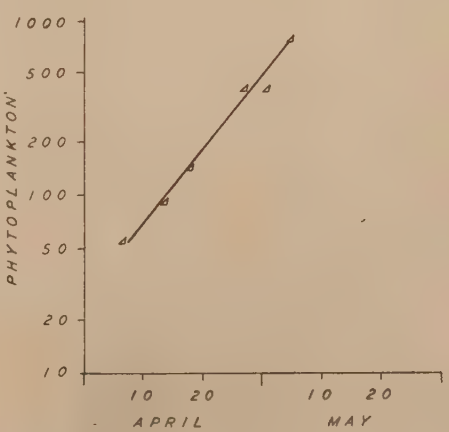

FIG. 4. Diatom crops sampled from the *Asterionella-Cyclotella* community on successive trips during the community's growth phase, plotted on a logarithmic ordinate. A doubling of the population every 7 days is indicated.

ing the course of the work have a bearing on this problem. Three possible sources are frequently suggested (Chandler 1940, 1942, Chandler and Weeks 1945): (1) shore erosion, (2) resuspension of bottom materials by storms, and (3) injection of turbid water from tributary streams. It seems unlikely that shore erosion would vary so much in different years as to cause the differences observed between 1949 and 1950, or that shore erosion could roil practically the entire western basin, as was the case in 1950. Resuspension of bottom materials also seems to play a minor role. If a sample of turbid water is allowed to stand, most of the turbidity remains after 24 hours, indicating that many of the particles are so fine they would not settle out in the western basin. The waters of western Lake Erie are apparently stirred from top to bottom by ordinary winds and currents, as evidenced by the absence of thermoclines, and by the uniform vertical distribution of phytoplankton (Chandler 1940). Fine particles would therefore be resuspended under ordinary conditions, not only by the storms of the rainy season. Moreover, there is good evidence that a strong northeast wind brings clear water into the island region (Andrews 1948: Table II, and Verduin 1951a). If resuspension were an important source of turbidity, the wind which drives such clear water should also roil it as it enters the shoal areas. Finally, the sharp lines between turbid and clear water suggest that injection of turbid water masses into the lake by the tributaries is the major factor causing the turbid areas described above. It seems quite likely that river water may enter the lake as a fairly thin layer flowing under or over the lake water, depending on its relative density, but the stirring action of winds and currents soon disperses the turbidity throughout the water column, thus roiling a much larger water mass than a calculation of river discharge would lead one to predict. The fact that average turbidities in the turbid areas amounted to about 25 ppm while the turbidity of the Maumee river during high water periods, for example, may be several hundred ppm suggests that the mechanism described above operates importantly.

Influence of Diatom Crops and Turbidity on the Food Supply in Western Lake Erie

The author has pointed out in a previous paper (1951a) that mobile sampling methods yield more reliable data on the growth and decay of populations than stationary sampling methods do. The decay curves for both 1949 and 1950 represent disappearance of diatom cells from these clear water masses, and do not represent displacement of diatom-rich by diatom-poor water. It is apparent, therefore, that the diatoms which disappear from the clear water settle to the bottom in the area occupied by the community. At no time were large numbers of empty diatom shells observed in the counting chamber, a fact which suggests that the cells which settle out appear normal under the microscope. Most of the organic matter contributed by a diatom crop, then, probably becomes available to the bottom fauna. No attempts have as yet been made to determine how large a fraction of the diatom crop can be accounted for by collecting the diatoms as they settle on the bottom.

The presence of turbid waters in western Lake Erie raises an interesting question: does the organic matter in the suspended material represent an important food contribution? The suspended material from a liter of turbid water has an ash-free dry weight of about 3 mg., which is only slightly less than the ash-free dry weight of the 1949 diatom crop (4.8 mg./l.). The percentage of organic matter in the suspended materials from turbid water is low, however (10–15%), while the diatoms contain 50–60% organic matter. If the suspended matter in turbid water settled to the bottom it would present a much more dilute supply of organic

matter than do the diatoms. But, as has been pointed out, many of the particles are so fine they do not settle to the bottom as diatoms do, so their contribution of organic matter if used at all in this area is used by the zooplankton rather than the bottom fauna. The problem warrants more detailed investigation than has yet been made at the Stone Institute.

Discussion

The comparison presented above shows that the contribution of the spring diatom crop to the food supplies of western Lake Erie varied markedly from 1949 to 1950. Although phytoplankton data for one or a few stations in the western basin have been gathered routinely over a period of more than 12 years, no reliable estimates of the diatom yields can be made from those data because the area occupied by the diatom communities was not determined. So it is impossible to say how frequently crop failures like that of 1950 occur. It is likewise impossible to judge whether 1949 represents a bumper or merely an average year.

This comparison was made possible by a radical departure from the stationary method of sampling. Many students of phytoplankton have shown a remarkable tendency to study the variations in vertical distribution in great detail while failing to determine the representativeness of their samples in the horizontal plane. In western Lake Erie surface samples can be regarded as fairly representative of the entire vertical column; samples at 5- and 9-meter depths usually differ from surface samples by less than 20% (Chandler 1940: Table X) but in any lake large enough to be stirred by ordinary winds, surface samples should be similarly representative of at least the euphotic zone, which is the important zone so far as photosynthetic yield is concerned. It seems likely, therefore, that a shift of emphasis from the vertical to the horizontal plane would yield significant information in other lakes also.

Estimates of phytoplankton yields, like those made above, are needed before a successful attempt to evaluate the importance of phytoplankton can be made. The may-fly populations in western Lake Erie, for example, vary greatly from year to year, but the influence of diatom yields on such variations cannot be studied unless the total crop is determined for the area in which the may-flies grow.

The term clear water, as used above, is definitely a relative one. The clear water areas were clearer than the turbid ones but turbidities of 12–15 ppm have a considerable light-absorbing effect, as is emphasized by the fact that 1% of surface light intensity penetrated to only 5 m. Compared to ocean waters (Clarke 1939) in which 1% of surface light penetrates to a depth of 50–80 m., the clear water of western Lake Erie would be considered highly turbid. Phytoplankton crops grow in this water by virtue of the fact that the basin is shallow; consequently the 5-meter euphotic zone represents one-half or more of the water column. If this clear water were 20 m. deep, growth would probably be as slow in it as in the turbid areas described above.

During both 1949 and 1950, the way in which turbidity limited the yield was the same; that is, diatom growth was inhibited in a turbid area which was apparently established before growth started. There was no evidence in these two years that a growing population was engulfed by turbid water which then terminated the growth phase of such a population. It is probable, however, that this does occur when a period of warm, clear weather is followed by rains, injecting large quantities of turbid water into the lake. Such water by flowing over or under clear water masses and subsequently mixing with them may extinguish the light in large portions of an established community.

The location of the 1950 community bears an interesting relation to the current patterns in western Lake Erie. Harring-

ton (1895) concluded, from a study of drift bottles, that waters circulate around Pelee Island in a clockwise rotation. Olson,[1] using drift cards enclosed in plastic envelopes, confirmed Harrington's observations. Consequently, water must be retained in the neighborhood of Pelee Island for longer periods than in the areas outside the region of rotation. The 1950 *Asterionella-Cyclotella* community was limited to waters around Pelee Island (Fig. 1). The fact that this water mass remained relatively clear while masses to the west and north attained prohibitive turbidities can, perhaps, be attributed to the influence of such a current pattern.

Summary

A comparison of the 1949 and 1950 spring diatom crops in western Lake Erie showed that the 1949 yield was 12 times greater than the 1950 yield. The difference was largely attributed to the greater extent of turbid water (apparently injected by rivers) in the western basin during 1950; the population density in 1950 was 40% of that observed in 1949. The 1950 pulse occurred a month later than in 1949, and a comparison of light and temperature data suggests that cloudy weather in 1950 may have influenced the tardy appearance of the pulse. Six datum points on the 1950 growth curve indicated a fairly constant growth rate, amounting to a doubling of the population every 7 days. The euphotic zone in the turbid areas represented about one-fourth, in the clear areas about one-half, of the water column. The former condition severely inhibited growth, while the latter permitted development of large populations. The ash-free dry weight of suspended materials in turbid water (3 mg./l.) was almost as large as that of the 1949 diatom crop (4.8 mg./l.) but much of the suspended matter in turbid water does not settle out in the western basin, as diatoms apparently do, so it does not become available to the same group of organisms. Yield studies of the kind presented here are an elementary step in any investigation of food relationships.

[1] Olson, F. C. W. 1950. The currents of western Lake Erie. Unpubl. doctoral dissertation. The Ohio State University.

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THE TOTAL MINERAL CONTENT OF LAKE WATERS

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The total dissolved solids or mineral content of lake waters has never been emphasized in limnological studies. In considering the chemical aspects of productivity, we tend to think at once of specific elements such as calcium, nitrogen, and phosphorus. There is reason to believe that in some waters one or more of these substances may be present in limiting quantities, and for this reason fertilization has been used in attempts to increase organic production in small lakes. It is possible that our preoccupation with individual elements has led us to neglect a simple and useful clue to the conditions which lie behind productivity. Recent studies in lakes of northwestern Canada suggest that the total mineral content of waters provides a rough indicator of edaphic conditions which must in some measure affect the productivity of lakes.

The range of mineral content in natural waters is exceedingly wide. A few small lakes in Maine, northern Wisconsin and Colorado are known to have between 15 and 20 p.p.m. of total solids (Clarke 1924a). Large lakes occasionally have between 30 and 60 p.p.m. but relatively few have less than 100. Most lakes with free inflow and outflow seem to have between 100 and 200 p.p.m. but as soon as the outflow is seriously restricted the total solids increase to 300 or more. Lakes with more than 300 p.p.m. of total solids are commonly described as saline, although they do not become obviously saline (e.g., to taste) until they contain two or three times this amount. In southern Saskatchewan, we find an array of saline lakes ranging from 500 to 120,000 p.p.m., the latter about four times the salinity of the sea. A general account of these saline lakes has been published (Rawson and Moore 1944). The present discussion will be confined to the range of mineral content in fresh waters.

The procedure for determining dissolved solids in lake waters is so simple that it requires little explanation. Samples of 200 to 500 cc. are usually collected. After settling or filtering to remove the suspended material, a sample, usually of 100 cc., is evaporated at 110° C. The residue, recorded in p.p.m., is usually referred to as total dissolved solids although it is recognized that some bicarbonates and some organic matter may have been decomposed by heating. Evaporation at 180° C. is sometimes used but this results in a further loss in the water of crystallization of certain salts.

Fresh waters are by definition dilute solutions and thus the minerals exist in a highly ionized condition. The total content of electrolytes can be determined with a suitable instrument and will provide a measure of the total mineral content. Rodhe (1949) has demonstrated the validity of this procedure for fresh waters of the commonly occurring carbonate type. In our investigations, it has been convenient to use the evaporation method since it is often desirable to use the residue for determination of one or more specific ions. When the major ions have been determined, it is convenient to plot them in the form of Maucha's (1932) "ion field diagrams" which make possible a quick visual comparison of different water types.

The Mineral Content in Alpine Lakes

In the years 1931 to 1940, limnological studies were made on a large number of alpine lakes in the Rocky Mountains and adjacent British Columbia. Some of these lakes appeared to indicate the relative effects of morphometry, climate and

geological surroundings on biological productivity. For demonstration purposes six lakes were selected (Rawson 1942). Three of these lakes, Paul, Okanagan and Minnewanka, were surrounded by soft rock and their waters had high mineral content—174 to 216 p.p.m. Two other lakes, Bow and Waterton, were in hard crystalline rocks and had low total solids, 82 and 85 p.p.m. Maligne Lake which has 104 p.p.m. total solids is in soft rocks but is subjected to a cold climate which may have slowed down erosion and the accumulation of minerals. A positive correlation was found between the total solids in the water and the average standing crops of plankton and bottom fauna in these lakes. An attempt was made to assess the relative importance of the edaphic, climatic and morphometric influences in these lakes. It was concluded that the edaphic factor (as indicated by the amount of total solids in the water) contributes to the productivity in each lake and that only in Maligne Lake is it suppressed or overpowered by unfavorable climate and morphology.

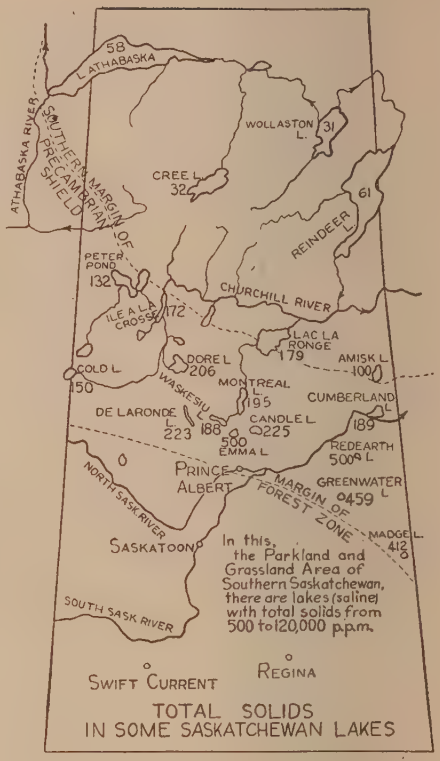

FIG. 1

LAKES ON AND OFF THE PRECAMBRIAN SHIELD

A large portion of central and northern Canada is marked by the exposure of a great shield of Precambrian rocks. One would expect that lakes on this area of hard rocks would contain less minerals than those whose basins and watersheds lie in soil covered and soft rock areas. This may be demonstrated by reference to the total solids in lakes of Saskatchewan, Figure 1. Lakes which lie wholly within the Precambrian area usually have less than 100 p.p.m. total solids. Lake Athabaska has 58, Cree 32, Wollaston 31, Reindeer 61, and Amisk, near the boundary, has 100 p.p.m. Lakes south of the Precambrian boundary but within the forest zone have from 100 to 500 p.p.m. In this area, if the lake has good drainage, i.e., continued outflow throughout the year, the total solids are between 100 and 200, but, as was mentioned above, if outflow is restricted, they soon accumulate 300 to 500 p.p.m. and become saline according to the arbitrary classification. Data from Saskatchewan lakes have been used for illustration but the condition is not local. Lake Nipissing and Lake Nipigon on the Precambrian shield have 60 and 114 p.p.m. Lake Simcoe and Lake Mendota, to choose somewhat familiar examples, have about 160 p.p.m.

While lakes on and off the Precambrian provide a simple and striking example, the procedure of relating the quantity and kinds of minerals in water to the composition of the substrate is capable of great extension. Möller (1949) has done this in a recent paper on minerals in the surface and ground waters of northwest Germany. This is an area of great geological variety, in which the substratum ranges from ancient granites to recent glacial deposits.

The Mineral Enrichment of Waters

The accumulation of minerals by river systems on the way to the sea has been approached usually from the broad aspect of geochemistry (Clarke 1924b) or in consideration of erosion and chemical denudation of the soil. It is desirable to consider also its significance in the productive capacity of lakes.

The maturing of a large volume of water can be followed in the Great Lakes drainage. Lake Superior, with much Precambrian drainage, is listed by Clarke (1924a) as having an average of 60 p.p.m. total solids. Lake Huron had 108, Lake Erie 133 and Lake Ontario 134. These values are averages from samples taken near the outlet of each lake at approximately monthly intervals in the years 1906–07. Analyses of samples from similar localities in the years 1934 to 1943 are provided by Leverin (1947). These averages show Superior with 60, Huron 114, Erie 165, and Ontario 161 p.p.m. Both sets of determinations show the general increase in mineral content from upper to lower lakes in the series. It is of special interest that after a period of about 35 years, the total solids of Lake Superior are unchanged while the lower lakes have apparently had a considerable increase in mineral content. It seems possible that increased erosion of areas draining into the lower lakes has been responsible for this accumulation of minerals.

The long-term fish production of the Great Lakes might be considered as rough evidence of their basic productivity. Over a 25-year period the fish production per unit area has been lowest in Lake Superior. The rate in Lake Huron is nearly twice that for Lake Superior, in Lake Erie about seven times and in Lake Ontario only a trifle greater than that of Lake Superior (International Board of Inquiry 1943). Obviously such differences in productivity cannot be correlated directly with the mineral contents listed above. Rather, the rate of fish production varies inversely with the mean depth of the Great Lakes. The demonstration is most striking in the comparison of Lake Ontario and Lake Erie which have similar mineral content, but Lake Ontario is more than four times as deep as Lake Erie. It would appear that the relative shallowness of Lake Erie (a morphometric condition) greatly outweighs the effect of the mineral content (the edaphic influence).

While the mineral content of a drainage system is expected to increase in the downstream direction, exceptions often occur and the interpretation of these irregularities may be of considerable interest. In a chain of lakes beginning in the Prince Albert National Park, Saskatchewan, Kingsmere Lake has 169 p.p.m. total solids. It drains into Waskesiu Lake with 188, on to Montreal Lake with 195 and thence to Lac la Ronge with 179. Lac la Ronge receives part of its inflow from the Precambrian and thus has lower mineral content than the two lakes immediately above it. Moreover, Hunter Bay, which connects with Lac la Ronge on the east by a narrow neck, has only 122 p.p.m. These determinations were made in 1950 after several years of what may be described as normal runoff. In the drought period of 1930 to 1936, and for several years which followed, Waskesiu Lake had little or no outflow and its total solid content increased from 180 to 200 p.p.m. In 1941 Lac la Ronge had only 137 p.p.m., presumably because it had received little water from the Prince Albert Park lakes in the previous 10 years. At the same time, and presumably for the same reason, Montreal Lake had only 166 p.p.m. Thus under special conditions reversal of the expected sequence of mineral content may occur.

Great Slave and Great Bear Lakes

Recent studies (Rawson 1950) have shown that the main body of Great Slave Lake has about 150, while Great Bear Lake has only 99 p.p.m. Great Slave has several times as much plankton and bot-

tom organisms as Great Bear and Great Slave produces from 3 to 6 million pounds of fish per year while Great Bear is judged (by Miller, 1947) as incapable of supporting a commercial fishery. This great difference in productivity is somewhat affected by a shorter season and lower temperatures. The main reason for the difference is thought to be the fertilizing effect of the Slave River. This river drains about one-ninth of the land area of Canada. Its average discharge into Great Slave Lake is 118,000 cu. feet per second. It carries about 170 p.p.m. of dissolved minerals and thus empties 60,000 tons of dissolved minerals daily into the lake. Great Bear Lake has no such inflow. Its drainage area is one-eighth that of Great Slave and much of it comes from hard Precambrian rocks.

Great Slave Lake and McLeod Bay

As if to demonstrate the effects of drainage and dissolved minerals on productivity, nature has provided at Great Slave Lake an experiment on a magnificent scale. McLeod Bay, off the long east arm, is the oversize "test tube"—90 miles long, 10 miles wide and 900 feet deep. Into this basin comes the runoff from an area of mostly bare Precambrian rocks, so the water of McLeod Bay has the amazingly low total solids of 22 p.p.m. Christie Bay of similar size and just across the Pethei Peninsula has 110 p.p.m. Christie Bay is broadly connected with the main lake (which has 150 p.p.m.) while McLeod Bay has a small outlet, Taltheilei Narrows, through which the flow appears to be constantly westward, i.e., there is no mixing back from the main lake.

The biological evidence for the difference in productivity between the two bodies of water is very striking. The standing crop of plankton of McLeod Bay is about one-half the weight of that of the main lake, the bottom fauna only one-seventh and the fish catch only one-quarter. It is true that the growing season is shorter by nearly one month in McLeod Bay than in the main lake but, since the mineral concentration supply is only one-seventh of that in the main lake, this is probably the main factor.

Conclusion

In studies such as those mentioned above, the determination of total solids has been found useful in relating the geological surroundings and drainage to the productive capacity of the lake. It provides a rough indicator of the edaphic situation for a particular lake and it is helpful in classifying lakes on a regional basis. Such determinations should not in any way be considered as a substitute for more detailed chemical studies. It is suggested, however, that the determination of total solids is useful and so easy that it could be made a routine practice even in the most casual of lake examinations.

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A COMMENTARY ON AMERICAN PLANT ECOLOGY, BASED ON THE TEXTBOOKS OF 1947–1949 [1]

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The idols and false notions which are now in possession of the human understanding, and have taken deep root therein, not only so beset men's minds that truth can hardly find entrance; but even after entrance is obtained, they will again in the very instauration of the sciences meet and trouble us, unless men being forewarned of the danger fortify themselves as far as may be against their assaults.

FRANCIS BACON, *Novum Organum*. 1608–1620. Book 1, Aphorism 38.

PROLOGUE

Both our decimal notation and our Christian calendar are arbitrary arithmetic conventions, the like of which come and go through civilizations. Consequently there is nothing particularly significant in the half century as spanned by the numbers 1900 and 1950, either in the world outside man, or of man. It is, therefore, only one of those gestures of a whimsical fate that turned the century in these States by ushering in a new science. Through the next fifty years that science developed in relative seclusion and isolation from the rest of the world, the story of which development is a drama of its own, with plots and subplots as well as intrigues. With a remarkable dramatic effect, the half century has been ushered out by a succession of four resounding chords, a climactic finale summarizing almost ideally the four principal themes of the plot. There may still be irrelevant codas, but when the curtains open again, there is every reason to believe that the stage will be much enlarged, beyond the confines of this country, and that new concepts and data will be in action, among them many which were but passingly mentioned during the act just completed.

Although history can never be written at the moment at which it occurs (only the events are taken down in writing), the events in American Plant Ecology are following so closely a pattern already laid by other more advanced sciences that the temptation is almost irresistible to see in the similarity the workings of a "natural law" for which we already know the later stages. In the words of some historians, "history often repeats herself." But let us go to the specific events.

American Plant Ecology appeared as twin births of European parentage at the University of Chicago; one child was allowed to be taken to a nursing home at the University of Nebraska before either was able to talk; there he received special coaching by his foster father so that he broke into speech before his twin. Although there has been a certain amount of inter-marriage and other relationships between the descendents, the two clans have remained in most cases politely apart, at least to this turn of the half-century.

Nebraska in 1893 was a grassland state, scene of a first botanical survey by the 19-year old Clements. In 1898 appeared "The phytogeography of Nebraska," by Roscoe Pound (who left botany to become famous in legal fields) and Frederic E. Clements. The last quarter of this book

[1] A condensation of this paper was presented at the VII International Botanical Congress, Stockholm, July 1950, for the author, by F. R. Fosberg. In the preparation of the complete version, the author acknowledges an unusual obligation to those who have read the manuscript and have given him the benefit of extremely valuable comments and criticisms: B. W. Allred, Murray F. Buell, Stanley A. Cain, W. S. Cooper, John T. Curtis, F. R. Fosberg, H. A. Gleason, Mason E. Hale, A. W. Küchler, W. B. McDougall, Henry J. Oosting, Walter P. Taylor, and Carol H. Woodward. I do not wish to imply that these persons are in accord with the views expressed. Their reactions run the gamut from high enthusiasm to high censure.

was a pioneer description of the "plant formations" of the state. Thus was born "Dynamic Ecology" which, followed by a half century of arresting publications from the fertile pen and mind of its sire, has collected a harem of adherents. To the rest of the world (who know American Ecology far better than we know non-American ecology), this body of knowledge *is* American ecology. In 1907, Clements moved from Nebraska to Minnesota. His decade of residence there has left little permanent impress, for on his departure the ecology was taken over by a worthy scion of the Chicago school, and that place has been for some time now its chief bastion. Frederic Clements' subsequent activities centered about Pike's Peak (Colorado), Tucson (Arizona) and Santa Barbara (California). Thus Rocky Mountain forests, southwestern grasslands, and chaparral, with grazing problems and watershed management, figure prominently in his writings.

Chicago in the 1890's concerns us mainly as the site of the young and lusty University of Chicago, and of the broad stretches of sand dunes on the southern shore of Lake Michigan—sands since serving as sites for industrial development. Henry C. Cowles came to Chicago in 1895 at the age of 26, and soon trod those dunes. The fruit of those excursions was "Physiographic Ecology." It was born in 1899 with the appearance of his "Ecological relations of the vegetation of the sand dunes of Lake Michigan." Cowles remained at Chicago until his death, quietly but effectively gaining the personal admiration and the scientific respect of a long series of students who have since made their own marks in the botanical world, and have themselves trained other students to become a third generation of teachers.

Nebraska's Clements and Chicago's Cowles represent strongly contrasting personality types, despite their similarities as co-founders of American Plant Ecology. Frederic E. Clements was a prolific writer of all-encompassing scope, a composer of textbooks, a solver of all problems, an establisher of complete systems and disciplines. Henry C. Cowles wrote relatively little, devoting his energies mainly to the training and development of his graduate students, through whom he still speaks.

It should not be thought that Frederic E. Clements and Henry C. Cowles "discovered" anything essentially new or "created" anything that had not existed before. The function of a "founder" of a "school" may or may not be associated with such primary conceptions. The basic foundations of American thought on the science of vegetation undoubtedly have not all been uncovered as yet. Human society furthermore invariably strews the way with stillbirths and arrested starts. Mendelian genetics, for example, waited from 1866 to 1900 before its birth was noticed. Buddhism languished in obscurity for 300 years before the monarch Asoka pushed it to prominence, and one wonders whether Christianity might not have died, as did many another minuscule cult built around a local Messiah, if Paul had not scattered its message along the shores of the Mediterranean.

In this small field of American vegetation, one should note among the earlier publications that in 1892 appeared Conway MacMillan's "The Metaspermae of the Minnesota Valley," with a discussion of succession in peat bogs. In 1894 J. B. Woodworth published "The relation of baseleveling and organic evolution," containing the germ of the idea that the development of vegetation parallels the development of the peneplain. In 1898 came C. H. Merriam's "Life zones and crop zones" which has had a long list of descendants of its own. In 1900 and 1901 T. H. Kearney published "The plant covering of Ocracoke Island; a study in the ecology of the North Carolina strand vegetation" and "Report on a botanical survey of the Dismal Swamp region." Both these publications might very possibly have mothered an empirical vegetation science had a Paul become interested.

Perhaps the most significant papers of the future still lie unnoticed on dusty library shelves.

In some respects, Americans have not advanced beyond a "natural history" stage of development. There is a confused conglomerate of interests, without the clear focus and precision of many of the Europeans, including not only those who have worked within one of the "schools" of phytosociology, but others as well, among whom are to be numbered those involved with the vegetation of Africa, Asia and Australia. This is not an objection against the Americans: it is a normal stage of growth. On the other hand, perhaps we should call ourselves "naturalists" and not "ecologists," for the term ecology has been long preempted in other countries for use in a strict etymologic sense, as a point of view and not as a subject matter. It is in this sense that the term ecology appeared in Braun-Blanquet's English edition of "Plant sociology," a most un-American application still blandly unnoticed in our thought.

The purpose of the present critique is to comment upon the four books referred to above as the four final chords that sounded at the end of this half century, the expression of a nation and of a period and not, for these purposes here, of four individuals. The *first* of these books is a group of selections from the writings of Clements, which though not designed as a textbook are so chosen that they represent all that is distinctively his Dynamic Ecology. Next, Cowles' Physiographic Ecology soon produced an offshoot that was concerned with individual plants rather than with communities of plants. The offshoot became known as "Autecology," and the parent by contrast became "Synecology." Autecology at first laid great weight on the microscopic structure of plants and the field was then known as "Ecological Plant Anatomy." Research in this Ecological Anatomy turned up data suicidal to itself, and Autecology saved its life only by quickly switching to an analysis of the environmental factors. Synecology and the newer Environmental Autecology have been refined and developed by several researchers, including W. S. Cooper at Minnesota. Cooper has been fortunate in finding two Pauls, and the *second* and *third* books in this tetralogy, by Daubenmire and Oosting, are restricted expressions of Cooperian Environmental Autecology and Synecology. Both Daubenmire and Oosting are to be commended for adding details and for final shaping of what has been to them the changeless philosophic structure they learned as students. The *fourth* and final book in this series represents an independent development, by an eclectic so to speak, who adopted the chief characteristics of both Chicago and Nebraska schools and interpreted them in terms of his own major contribution, an elaboration of the concept of symbiosis. This is W. B. McDougall, and what we might term for present purposes his "Symbiontology." These four volumes are a fitting culmination to the first half century of American Plant Ecology, and were they written to order for the purpose, they probably could not be improved. They form worthy and notable contributions in that they so brilliantly crystallize the endemic and individual nature of American Plant Ecology that that nature, now visible, may find less reason to exist as a distinct development in science.

One of the commonest criticisms of the reviewers of the manuscript of this paper was that I comment upon American trends on the basis of only four books, three of which are textbooks for beginning students, not works for the professional ecologist. I state without hesitation that in my personal opinion these books are representative, and would not be materially altered were they revised for professional uses by their authors. It is a matter, I admit, of pedagogic principle as to whether or not beginning students should be exposed to, and can benefit by, divergent viewpoints. I confess I am, both in theory and practice, an adherent of that absurd notion that courses in com-

parative religion and in sectarian theology can be equally intelligible to our college students. I prefer that they receive the former. I look upon this small field of vegetation as Mortimer J. Adler (1950: 91) would sweep the entire field of human knowledge in a *Summa Dialectica*. As he "sees it, a modern *summa* would be an attempt, not to umbrella the world with a dogma or a fixed philosophical system, but to create an understandable discussion of the fundamental issues."

The comments on these four books are not to be considered primarily a review of their factual contents and a spotlighting of the good and bad in omission and commission. To the contrary, the comments are in the nature of a critical analysis of certain methodologic and epistemologic foundations of American Ecology. The immaturity and artlessness of some of these foundations deserve serious scrutiny in these times that have seen the rise of Nazi physics and Soviet genetics. As Americans, we bugle our claim that totalitarian straight-jacketing of the scientific intellect destroys science. It follows as a corollary that freedom of the scientific intellect is a precious privilege, and those who possess it have a deep obligation to exercise it for the advance of science. It comes as a curious anomaly therefore to find evidence of a self-imposed imprisonment on the part of some scientific workers, with apparent contentment on their part. If such scientists can accept so placidly the control of their thoughts by traditional dogma, one wonders whether they might not accept with equal placidity the control of their thoughts by governmental decree. Nor should we deem such acceptance impossible of happening, on the mere grounds that our own science, being "free," is for that sole reason, valid and "true," whereas a nationalistic decreed science is, ipso facto, falsehood and error. "The floating of other men's opinions in our brains makes us not one jot the more knowing though they happen to be true," as timelessly phrased by John Locke in 1690 (I: 4: 24). Safeguard for any free science lies ultimately in the individual, not in society. It lies not so much in whether facts or pseudo-facts are presently floating in our brains, as in the exercised ability of our free minds to question and verify our thoughts, and to mold them into new forms as occasion warrants. Knowledge, therefore, is really possessed by the individual (and thus by his science) only insofar as he himself comprehends the methodologic and epistemologic restrictions of that knowledge.

Albert Einstein, in criticizing modern physicists for lack of interest in the greatest and yet unsolved problems, speaks for all scientists, not excluding ecologists. He writes (1950: 13), "There exists a passion for comprehension, just as there exists a passion for music. That passion is rather common in children, but gets lost in most people later on." In those years of "later on," there are many men whose ideas and habits of thinking are so firmly ingrained that neither the clearest logic nor the subtlest persuasion will lead them to reconsider their viewpoints, and thus return them to that period of uncertainty and even intellectual chaos which antedated their present reign of calm. I am reminded also of James B. Conant's comment concerning the way science once advanced a step. He writes (1947: 15): "Seventy-five years ago the Professor of Natural Philosophy at Harvard told his classes that 'people now accept the undulatory theory of light because all those who formerly accepted the corpuscular theory are dead." For "those" men, not yet dead, this paper is not intended. If among the others, there are some who take offense—even though no effrontery is meant—let them ask themselves to what degree their injury may be related to a subconscious realization of their own weakened foundations, and to an attempted reattainment of security by a buttressing with affirmation and counterattack. In the pages that follow, let it not be said that this is an attempt to impose an Eglerian opinion upon those who are in the field of ecology. I have nothing completely new

to offer here, to replace that which I criticize—a point which nonplussed many of the reviewers of this manuscript. My aim might be called Socratean, but not Aristotelian. I am hoping to write that which some electronic calculating machine might turn out if one were constructed to deal with concepts, and if the four books under discussion were fed into it. I write with three designs upon the individual reader: I ask him to question his own beliefs in the field of ecology, in an attempt to realize the limitations of them. I ask him to try to comprehend (even if he does not agree with) the beliefs, opinions and language of those with whom he thinks he has a controversy. Lastly, I ask him to write and talk in a language that is not only understandable to those of his own clique, but that does not invite misunderstanding from his professional adversaries.

We all recognize that vigorous discussion is essential to such scientific advance as follows upon a remolding of the old beliefs. Such discussion is invited, not as a punch-by-punch affair, one punch in each issue of a journal and each punch aimed as a knockout, but by correspondence and formal symposium.

Above all, I ask that the reader call my attention to errors in fact or reasoning which he may spot in this paper. My intent is to aid the science of the future. Though my mode of aiding may be unconventional, it is that which has evolved after two decades of otherwise unsuccessful struggle with this very same environment of our science and our scientists.

I. Dynamic ecology

Clements, Frederic E., selections from the writings of, compiled and edited by B. W. Allred and Edith S. Clements. DYNAMICS OF VEGETATION, xxiii, 296 p., 70 pl., glossary, index. H. W. Wilson. New York. 1949.

> The content of this book . . . represents a broad philosophical outlook, combined with practical experience that should make it a worthwhile contribution to scientific knowledge and its practical application.—From the Preface, by B. W. Allred.

The volume is composed of eight chapters, each being a reprint of a distinctive paper, chapter, or collection of reprints on a unified topic. A cursory glance at the Table of Contents shows at once the strikingly split personality of Frederic E. Clements. On the one hand we have Clements the practical realist, the Clements who impressed the soil conservationists, agronomists and range managers with his down-to-earth understanding of land management, the Clements who could discuss and write convincingly about such problems with almost complete absence of technical terminology and intellectual gyrations. On the other hand, we have Clements the uncompromising idealist, the speculative philosopher, driven by some demon to set up a meticulously orderly system of nature, as neatly organized and arranged as the components of Dante's Inferno. It is easy to see how Clements gained the respect and enthusiasm of the practical field man, who would then "accept" the complicated philosophy, not as something which he really comprehended, but as something which must be "right" since it came from Clements the realist.

Chapter I, Plant Succession and Human Problems, is a fitting introduction to the dual role of this book. The first half discusses the kinds of succession, in water, on rock, on soils. The second half introduces such problems as erosion, floods and overgrazing.

Chapter II is the only discussion of actual experimentation, of the planting of various species under different conditions, and observations of the resulting variations in growth. The scope of these investigations (p. 24) seems to be as broad as the whole field of agriculture, or broader than it; and the reader is left wishing for simple observational data on which he might base his own conclusions, rather than having a discussion of the "true nature of plant competition," with dogmatic affirmations

as to its role in the differences between species, and in the development of climax communities.

Chapter III (Plant Indicators), IV (Nature and Structure of the Climax), and V (The Relict Method in Dynamic Ecology) have much in common. They are written by Clements the speculative philosopher, and show his extraordinary ability to take an idea, organize it, break it down, classify it to a degree of minutiae that not only leaves nothing for anyone else to do but defeats its very purpose by giving us ultimate particles which are identical with those we already know. The concept of plant indicators, for example, had been originally a very valuable tool in the practical applications of vegetational knowledge. Then Clements began to see an indicator of something every time he looked at a plant community. The mere listing of the major kinds of indicators occupies two pages of the Table of Contents. Some of them even he must admit are expressions of organizational redundancy, as when he says (p. 58) that "a community of trees is . . . an indicator of forest" and (p. 80) "grazing indicators furnish a decisive test of the desirability of utilizing them." When we get through all such extraordinary elaborations of the obvious we realize more fully that vegetation is a highly complex system, in delicate adjustment with itself and its environment, and as such, *any* characteristic of it is an indicator of various other characteristics. Having reached that generalization we see no more need for a detailed description of the kinds of indicators: we want a fuller description of vegetation itself.

In Chapter IV, The Nature and Structure of the Climax, we find Clements at his philosophic and terminologic optimum. The idea of the climax community is quickly enlarged to become the climax formation. (Clements never does segregate these two concepts, and swings maddeningly from one to the other according to the exigencies of his thinking, and just when we believe he should have checkmated himself.) The climax is *identified* with climate and physiognomy, thus supplying two of the most characteristic features of the Clementsian speculative philosophy. We are then subjected to an orderly breakdown of the climax, carrying us through a sequence of -ations, -es and -ules, of associ-, consoci-, faci-, loci-, soci-, lami- and sat-'s, in all their devious combinations. This pigeon-holing of nature is as orderly and thorough as the packaged and shelved organization of a gigantic food mart. One might be perhaps amazed also at the extent of our vegetational knowledge that now permits such precise nomenclatorial application! No sooner have we adjusted ourselves to this broad outlook on the climax than we suddenly realize that this climax *is* vegetation, is all of vegetation, is completely synonomous with "vegetation." So why use the word? And if we do wish to use it, we are back again to that favorite American query "What is the climax?"

Chapter V analyzes the relict concept. There was a time that a "relict" was a very respectable plant community, something, for example, left behind in a bog after the retreat of the glaciers. As such, it was totally out of adjustment with its present new environment (and thus negated one cardinal tenet of ecologists—that vegetation was not only in intimate relation with its existing environment, but was the very effect caused by it—a situation which for some strange reason did not disturb their equanimity). Clements extended the concept to include communities which had survived some important environmental change (*i.e.,* were lagging in their own change behind that of the environment) and those which were persisting because of some compensatory factors in their environment. His analytic mind went to work, and everywhere he looked he saw relicts, 40 pages of them in this volume. We reach the end of this chapter, and then realize abruptly that all vegetation is relict vegetation, that it is meaningless to refer to any particular community as a relict. It is true that we have a slightly enlarged understanding of vegetation, that as a nat-

ural phenomenon it has a history. We can, with discernment, read the evidences of that history in what we see today. The term relict, however, like the terms indicator and climax, has been stretched to soap-bubble thinness so as to cover all the world's vegetation. One gentle sneeze, now—the bubble is gone—vegetation is as it was. When is a relict not a relict?

In Chapters VI, VII and VIII Clements the practical land manager returns, and we find empirical and objective discussions of problems in land management that concern soil, forage, forest, and water. Although dogmatic assumptions can frequently be found on which others might differ in opinion, they are spotted easily, and do not interfere with the continuity of the factual objective data. In these chapters, as well as with most of Clements' writing on these topics, especially in the 1938 text, we find a command of the English language, a gracefulness and fluidity of style which is distinctly superior to that frequently found in works of this kind. Although such matters as style might not be noticed by all readers of this literature, it is very possible that its subconscious influence has done much to gain the acceptance of the man and of his ideas.

Clements gave little evidence that he was a philosopher with grounding in the cultural heritage of European philosophy, or a methodologist with grounding in academic logic and scientific method. As such, he fell heir to all the pitfalls that a better knowledge of history might have revealed to him in advance. He was a classifier of concepts who so thoroughly splintered his ideas in order to classify the splinters that the ultimate particles became the same whether the splintering was done on the basis of indicators, relicts, climax or phase of succession. On the other hand, he never let the ritual and dogma of his pseudo-theologic system interfere with his common sense in applying remedial measures to an eroding hillside or an overgrazed range. Now that he has gone, it remains to be seen whether his followers will grasp the meaning behind his words, and whether they will wrangle interminably over the forms of terminologic baptism and the particular phrases associated with their communion with nature; or on the other hand, whether they will retain the core and meaning of what he has revealed in man's relation to his environment.

II. Environmental autecology

Daubenmire, R. F. PLANTS AND ENVIRONMENT, A TEXTBOOK OF PLANT AUTECOLOGY, xii, 424 p., 16 t., 87 f., index. Wiley. New York. 1947.

> . . . restricting the material to this branch of ecology . . . [will permit] a student to devote his entire energy to a study of fundamentals without having to sacrifice a large share of the time to the mastery of any of the several conflicting philosophies of plant sociology. . . . Also, in deference to students of intermediate status, the citations are restricted to papers written in the English language.—From the Preface.

This volume, a portrait of one of the four conflicting American philosophies, comprises one short introductory chapter; seven major chapters on the seven environmental factors recognized by this author; and two short concluding chapters on the interrelations of these factors, one on adaptation, the other on evolution of species. Thus we have a picture of Daubenmire the environmentalist, who admirably brings to sharp focus one of the strongest trends in American Plant Ecology. This trend is a pendulum-like backswing from the days when anthropomorphism and teleology were rampant. In opposition to those ancient days (p. 365), "truly scientific methods of reason and experimentation were substituted for the method of speculating upon non-experimental observations." It was then necessary to accept "the principle that causes produce effects and these in turn may become causes, the cardinal tenet of ecology by virtue of its very name" (Clements: 163), and to follow this up with the principle that all causes are inherent in the environment. These last

two principles have been accepted with bovine placidity by too many Americans, and their extraordinary speculative and assumptive natures will apparently require a Quixote before seen in their true light. The next step followed automatically (p. 2): "The environment may be analyzed into a number of factors, such as soil, moisture, wind, and temperature. . . . In fact, any force, substance, or condition which affects organisms in any way becomes a factor of their environment, and the sum of all such factors constitutes environment." In order to keep within the bounds of "truly scientific . . . experimentation," emphasis has been placed on instrumental analysis of the environment. Such analysis has unwittingly put great weight on the normal, average, mean, and continuing aspects of that environment, at least through the course of and within the limits of, the experimentation. It has relegated almost to nonrecognition the significance of catastrophic, abnormal, extreme and accidental aspects of the environment. (See Fig. 49, p. 233, for a correlation of seedling survival and seasonal soil moisture, and the use of that average-season correlation apparently to "explain" altitudinal vegetation zones, without considering the possible importance of cycles in annual precipitation.) This one-factor average-environment causationism is the speculative philosophy upon which Environmental Autecology is precariously balanced.

The seven chapters on separate factors (soil, water, temperature, light, atmospheric, biotic and fire) are without doubt admirably written, well organized, thoroughly annotated, and highly suitable as a source of reference for the great mass of detailed information that can be segregated under these headings. The hierarchically arranged list of headings at the beginning of each chapter is a marked advantage to the reader and is a feature that could well be followed in many other texts. On the other hand, the use of small raised numbers for reference to citations is a matter either of unawareness of pedagogic potentialities, or a veiling of unsuitable citations. Although it may make a fine impression to see these numbers scattered liberally throughout the text, and it may save a certain amount of space to use them, it does on the other hand hinder the student from becoming acquainted with the leading researchers in the field and with the recency of their writings, and it does prevent the professional reader from verifying easily the author's statements in terms of the literature familiar to the reader (as when the whole section on lichens is supported by a reference which on checking we find to be the Chicago ecological anatomy text (Coulter, Barnes and Cowles, 1931)—hardly a valid reference in the face of several existing summarizations of lichenology).

In the penultimate chapter, "The Environmental Complex," the author passes to the consideration that (p. 345) "factors never operate separately or constantly upon the organism, that environmental relations are at once complicated and dynamic." In 11 pages (as opposed to 340 pages of "one-factor ecology") he discusses well, but all too briefly the cannot-be-overlooked literature on interacting, compensating, optimum and limiting factors. One, however, is not quite certain that Daubenmire convinces himself of the unity of the environmental complex, especially since his only illustration for this chapter is a photo of deformed trees at a forest edge on San Juan Island, Washington, presumably reacting to an environmental complex, yet concerning which he says that (p. 353) "the real cause for difference in vegetation appears to be edaphic." One-factor ecology is psychologically *so* satisfying!

The final chapter is a cautious discussion of adaptations, interesting from a historical point of view, for it represents the squeezed out remnant from the heydey of "ecological anatomy," when anatomy and environment were mirror images of each other (just as climax and climate are now considered to be, on similar

pseudo-religious grounds). The chapter closes with a full discussion of Turesson's work on genetic and ecologic units in floristic taxonomy, while the more recent studies of Clausen, Keck and Hiesey are passed over by the bare statement, with references, that "subsequent work . . . has . . . verified the correctness of his views."

The bibliography lists 612 English language titles, including one Japanese paper. Six per cent are from the British Empire.

In the style of writing, this volume is in marked contrast to Clements' volume. Daubenmire has succeeded to a high degree in developing a terseness, a paucity of words, a fact-crammed grammatical structure that is the goal of many a scientific writer. It is as functional, as devoid of decorative flourishes and artistic ornamentation as the layercake skyscrapers built lately in New York. As was said by the romanticist against the classicist, his writing had become correct and soulless, learned and uninspiring, scientific and godless, virtuous and cold. One can almost imagine that this author, beginning with terse abbreviated lecture notes, kept building through the years in card-catalogue style, inserting abstracts and summaries in their appropriate places as the new literature appeared. For these reasons, the book will long serve as a well-organized reference work for the American literature on the effects of environmental factors on plants.

III. Synecology

Oosting, Henry J. The Study of Plant Communities. An Introduction to Plant Ecology, 389 p., 190 f., 11 t., index. Freeman. San Francisco. 1948.

> Although controversial issues are not deliberately obscured, they are not emphasized. The assumption has been that a beginning student should acquire a working knowledge and appreciation of the field before he is introduced to matters that might confuse him.—From the Preface.

> *Autecology* is not always distinguishable from some kinds of physiology; in fact, there is probably no point in doing so. . . . Autecology is, nevertheless, justifiable because of the contributions it can make to synecology.—Page 17.

This volume, painting the synecologic version of the controversy, is composed of five parts: an introductory chapter; three chapters on the nature of the plant community on quadrat sampling and on community form and structure; four chapters on environmental factors; three chapters on developmental changes in vegetation, on the geography of vegetation, and on the history of vegetation; and a final chapter on the practical applications of the pure science of Synecology. Thus we have a picture of Oosting the synecologist, who has collated and organized his excellent command of the pertinent literature, to draw for all of us a detailed portrait of that speculative philosophy that can be known as Synecology.

Both Synecology and Autecology can be found in Cowles' earliest writings, although apparently they did not attain their mature state until Physiographic Ecology ceased to attract interest as a single unified field. Synecology borrows heavily of the one-factor uniform-environment causationism of Autecology, and has absorbed into itself a considerable amount of Clements' Dynamic Ecology. The speculative foundations of Synecology are not apparent on the surface, and in fact may be entirely missed by the hasty reader, since all "controversial issues . . . are not emphasized." As happens so often, a controversial speculation is what the *other fellow thinks*: fundamental real basic facts are what the *writer knows are true*. In this case the truth follows party lines closely, and is supported by such a wealth of accessory data and excellent illustrations that even the deepest disbeliever will read the book with pleasure and profit.

The volume opens with an annotated question, " 'What is Ecology and What Good Is It?' ". The book closes with another quotation, " 'The social function of

ecology is to provide a scientific basis whereby man may shape the environment and his relations to it, as he expresses himself in and through his culture patterns.'" Without any reflection on the worthiness of these beginning and ending quotations, one naturally wonders if the rest of the book is not equally a compilation of quotations, express or implied, making of it—as perhaps was the intent —the product of the decade and the voice of Synecology.

The first chapter, Part I, discusses basic ideas on the discipline of Synecology. A section begins "An organism without environment is inconceivable," and thus we are introduced to the powerful all-out environmentalism that is ecology. The next section starts by saying that "Environment includes everything that may affect an organism in any way. It is therefore, a complex of *factors*," and though the author later dwells on the interactions of these factors, the antiholistic approach is boldly adopted. This leads him to say in the next paragraph that "Since all plants and animals, including man, are organisms, and since environment can at times include almost anything in the universe, the subject matter of ecology is almost unlimited." This nebulous unlimitedness is highly characteristic of American thought, and though it seems to delight the ecologists, it is a circumscription that has not yet gained the respect of other biologists. Later, in the discussion of the history of plant ecology, we meet the now-time-honored ancestry of the Chicago school: Humboldt, De Candolle, Grisebach, Drude, then Warming and Schimper. The interesting feature about this history is that it *is* so! Nothing more! Cowles drew primarily upon Warming, fertilizing it by his own fecundity. Thereafter, physiographic ecologists drew what they could from Cowles, and increments from outside or rebirths from within have been almost negligible. Following this, Oosting's distinction between Autecology and Synecology has a rather novel twist, in that Autecology is defined as dealing with individual organisms *or individual factors,* and Synecology, with plant communities *or factor-complexes*! These definitions only emphasize the more the American confusion in the use of the same word for both a point of view and a subject matter. Regardless of this holoid definition of Synecology, Oosting finds that (p. 75) "it is logical to approach the subject . . . through individual factors and their effects"! Then comes a discussion of the threadbare subject of "static and dynamic viewpoints." American ecologists have told themselves with pleasure and pride, and through more than one generation, that they have developed a highly superior "dynamic approach," in contrast to the restricted "static approach" of the Europeans. Now it is quite true that the Europeans have nothing to compare with our grandiose terminologic and conceptual flights of everything up to continent-wide cli-seres, but I am not sure we should boast about them. Furthermore, even a cursory glance at the European literature of today or yesterday will reveal a sensitive but sturdy grasp of the developmental characteristics of vegetation.

Another feature of Synecology is presented on the first page of the following chapter (p. 21), where the idea of the plant community is extended from the "concrete community" to the "abstract community." This idea of the "concrete" and the "abstract" was discovered by ecologists midway through the half-century, and much ink was used, both in published papers and questionnaires. It has come down to us now a quarter of a century later in this greatly abbreviated form, devoid of such words as comparison, abstraction, generalization, induction and concept. The surprising feature is not that this idea of the ecologists has survived in such a vestigial form, but that it was necessary ever to mention it in the first place. This phase of scientific method, known to Aristotle and developed again by Berkeley, Hume and Locke, is one of the most basic precepts of logical reason-

ing, one that should exist as a second nature to all scientists. It is hardly an idea that should form the subject of discussion and of delayed acceptance in the twentieth century. One must (or should one?) assume that Oosting's skeletonized reference to this episode is all that he considers necessary for the students of today, who are presumably better grounded in the principles of inferential reasoning than those of a generation ago.

Part 2 is entitled "The Plant Community," and deals very satisfactorily for most purposes with certain basic characteristics of communities, with their various structural features and with the quadrat sampling necessary for describing those features.

Part 3 admits openly the environmentalism of Ecology in the title "Factors Controlling the Community: the Environment." Four chapters give a readable and interesting survey of the influences of the various factors on the phenomena of plant communities. It is somewhat confusing to find half of one chapter devoted to a discussion of "plants as factors," *i.e.*, the relationships of plant to plant within a community. Its inclusion here is a fundamental confusion of what is "inside" and what is "outside"; of what is vegetational "anatomy" or even "physiology," and what is "environment." Thus we have still another line of evidence that Synecology is not yet consistent as to the level of integration of the phenomena it is investigating.

Part 4, "Community Dynamics," involves a strange use of the word dynamics that would seem to stem directly from Clements' Dynamic Ecology. The first chapter deals with "Plant Succession," with its causes and kinds and stages. We hear about the time-honored and simple "primary succession" and "secondary succession," but there is no mention of the increasing data from the tropics to the Arctic that will eventually demand a reorientation of thought toward a more complex development, involving primitive and civilized populations; and continuing postglacial changes of floristic edaphic and climatic adjustments. Here we find also a discussion of the monoclimax and polyclimax theories, a development that belongs to both Nebraska and Chicago schools. I have not traced the monoclimax to its origins in the literature. It appears to be an intellectually atrophied vestige of Cowles' original and long-forgotten discussion of the climax. Cowles' desirable and mature concept did not survive; it was replaced by the much simpler monoclimax. The monoclimax seems in part to have been set up only to have been knocked down by the polyclimaxists, who have been the "splitters" of the ecologic world. In my opinion, whoever talks about monoclimaxes and polyclimaxes in unaware of Cowles' lucid discussions—or maybe is intellectually incapable of grasping Cowles' concepts. In another direction, Oosting recognizes most of the Clementsian climaxes, and then adds climatic, edaphic, physiographic and pyric climaxes. This contribution of the synecologists is a perfect reflection of their one-factor environmentalist philosophy. The mode of thinking was brought out excellently in a report of a field trip to the New Jersey pine barrens (Ecol. Soc. Amer. Bull. 29(3) : 55–57, 1948). It was considered a distinct advantage to have present on that field trip the leaders of the two opposing theories on the barrenness of the barrens, one considering fire to be the cause, the other considering the sterile soil to be the cause. That these two "factors" might be integrated into a single indivisible holistic unit was at least not implied in the written report. As Stanley Cain once remarked, the "climatic climax" in many cases is but the "edaphic climax" of the most favorable sites of the region, and one term is no more valid than the other. This challenge, however, to the lack of logic in the mono-factorial nomenclature was never accepted.

The chapter on vegetation geography is an excellent survey, finely illustrated, of the various vegetation types of the United States. The chapter on the history of

vegetation emphasizes the pollen-analytical, dendrochronologic and relict methods of obtaining historical data.

Part 5 is an interestingly written survey of contemporary land management, of forestry, grazing, soil conservation, watershed control and related fields. That this material is segregated and placed at the end is not necessarily undesirable. It is merely indicative of the historical development of the science, for ecology has long prided itself in some quarters for being a "pure" science, of no practical value. The practical aspects have been tacked on recently, and have not yet been assimilated into the body of the science.

The bibliography lists 276 titles of which seven are in a foreign language. Of those seven, six are 19th century works referred to in the discussion of the history of plant ecology. Of the 269 English language titles, all but ten are American, and seven of those ten are English.

Oosting's style of writing is less compact than that of Daubenmire, and one can read it with a greater sense of relaxation, despite his use also of citing references by numbers. Within the framework of the concepts of his Synecology, and under his partisan uses of many words in chapter headings, he develops a fascinating and interesting story that is well documented with the detailed American researches of recent years.

IV. Symbiontology

McDougall, W. B. PLANT ECOLOGY, fourth edition, 234 p., 118 f., index. Lea & Febiger. Philadelphia. 1949.

> Although many excellent papers and some books on ecological subjects have been published during recent years, most of them have not changed our fundamental thinking to any great extent.—From the Preface.

The volume consists of twenty-two coordinately ranking chapters, which, only after thorough acquaintance, reveal themselves as segregating into three or four major groups. Once those groups are recognized, the basic structure of the volume appears and allows us to compare its particular brand of speculative philosophy with the preceding. McDougall has taken some basic features of both Dynamic Ecology and Synecology, and fused them with his own personal addition, an extended and enlarged concept of "symbiosis." This all-embracing symbiosis in my opinion is a distinct and valuable contribution to American vegetational thought, even though for these purposes it might be considered grossly overdeveloped. Until one has considered it, accepted its values, realized the enlarged horizons that it gives us of natural phenomena, and until more satisfactory principles are discovered, it is short-sighted and unreasonable either to ignore it or discard it.

The school of Ecological Anatomy in a suitable modern version is covered by the first three chapters, on roots, stems and leaves, respectively. To this group should be added Chapter VI "Pollination," treating of adaptations for pollination by the environmental factors of animals, wind and water. Chapter XV, "Growth Habits of Plants," is the gross morphologic aspect of this same problem, "to classify plants into life-form groups and to interpret these groups in terms of the environment."

Environmental analysis is treated in Chapters X through XIV, on light, heat, air, soil, and water, respectively. There is no separate discussion of the interactions of factors.

Numerous and miscellaneous types of symbiosis, of plants with plants, and plants with animals, occupy Chapters V, VII, VIII, and IX. These include what others term zoologic factors, and "internal" botanical activities of the plant community.

Synecology, called "social disjunctive symbiosis," is covered in Chapters XVI through XXI, and we recognize the customary subdivisions into: the nature of the community, structure, classification, plant succession, and geographic distribution in the United States. Much that stems from both Nebraska and Chicago schools is included here, concerning both

terminology and concepts, for which further discussion at this time is unnecessary.

The final chapter is entitled "Applied Ecology," and we again suspect that the applied aspects of the science were grasped as a later stage in the ontogenetic development of its author, and have not yet been integrated and assimilated through the body of the volume.

References are distributed at the ends of the chapters. They are all in the English language, including one Japanese reference, one Philippine paper, and about 35 British titles, a relatively high proportion of the total in comparison to other American texts. In this and the previous three analyses of the proportions of foreign references, it is not implied that British or foreign-language references necessarily have a place in an elementary textbook (though I have found many men who could use them, among the students). An interesting correlation however is noted between the Americanism of these bibliographies and that of the philosophic substructures of the books themselves.

This is a shorter book than Oosting's work, at least in number of pages, and is suitable for a shorter course. It has an equally readable style, is well illustrated, and even though it has not changed significantly since the first edition of a quarter of a century ago, it expresses very adequately the American point of view toward vegetation.

Epilogue

The history of a science may be likened to the life histories of certain insects. There is a period of accretion and assimilation, during which the body increases in the weight of its constituents and begins to strain at its non-elastic chitinous enclosure. Then comes a sudden breaking and splitting. A new insect emerges, different in fundamental respects. The story is repeated, and this new organism adds to itself more of the material of which it is composed. Sciences likewise go through long periods of patient plodding accumulation of data. These are tacked onto the basic framework of the science, until sometimes it groans with the burden of carrying such a multitude of minutiae. Then suddenly there is a revolution, an upheaval. We can use another simile, that of the kaleidoscope of our childhood days, a mirror-lined box, in which we could see the pattern produced by colored glass particles. A slight jar, and the pattern is suddenly rearranged. An entirely new design appears. With a science, nothing new is added, but all the data suddenly become reoriented, and a new structure appears, based on entirely new concepts. Physics has gone through several such metamorphoses, and its workers are prepared for more. A first-class man of science normally contributes both new concepts and new data to the growth of his science. Furthermore he realizes—or should realize—that his theories and his concepts are to be modified by the next generation and he should welcome the activity of students who appear destined for this step. Some American ecologists however have felt they have attained "reality" and all that is now necessary for themselves and their students (who have inherited this sense of finality) is to go on adding details to the old conceptual structure. Thus American Ecology has been stuffing itself with such "facts" for half a century, and in the neatly appropriate year of 1950, it is showing some cracks in its chitin. Even though the cracks can be seen only from certain vantage points, and even though history may do the unpredictable in giving us tomorrow an imago totally unvisioned today, still a glance at these contemporary cracks may have an advantage for that coming generation which may be destined to burst the seams. Let us hope those seams are burst, and the organism is not strangled by the very walls which were once an enlargement for the younger organism.

The circumscription of the field of ecology is beginning to interest various workers. Increasing quantities of biologic

data have resulted in an increasing number of textbooks on the subject. A comparison of these books, however, both in this country and abroad, shows a remarkable divergence in the materials covered, a divergence that is getting to be looked upon as a fault, not a virtue. Richards (1939) captures this idea in his review of an animal ecology text when he says that "The difficulty of writing a satisfactory book on ecology lies in the lack of any agreement as to what the subject is really concerned with. The definition 'Ecology is the branch of biological science that deals with relations of organisms and environment' would provide the title for an encyclopaedia but not delimit a scientific discipline."

It is not only the indefiniteness of limiting its subject matter that characterizes American Ecology. There exists also a remarkable naiveness toward our European cultural heritage in the realms of *scientific methodology,* applied logic, and the philosophic foundations of the exact sciences. Our attitude toward scientific research bears a certain resemblance to that of the layman who divides all knowledge into the vagaries and speculations of metaphysics philosophy religion and the occult on the one hand, and the incontrovertible immutable "truth" and "reality" that is the realm of the experimental scientist on the other hand. With data from an atmometer, a quadrat, and a microscope, ecologists "know" nature; and are satisfied. We find, for example, such an illuminating statement as Daubenmire's (p. 358) that "Morphologic characteristics should always be subjected to physiologic experimentation . . . for interpretations based on human logic cannot be relied upon." Oosting adds (p. 232) that "It is often possible for honest observation to be wrong, and only quantitative and qualitative data will demonstrate the discrepancies. . . . When questions of 'why,' 'when,' or 'how' come up, they can be most satisfactorily answered with absolute data." These revealing phrases recall F. S. C. Northrop's words (1947: 177), "It is usual for the popular mind and occasional uncritical scientific minds to assert that science is concerned only with fact in the sense of what can be observed [directly, or from the reading of instruments] and that it has nothing to do with theory." One readily understands and sympathizes with many present ecologists in their adverse reactions to some of the hypotheses of earlier workers that were found to be untenable after subsequent research. But one does not for such a reason dispense with the whole of theorization—nor does he sell the automobile after the wife establishes its first contact with the garage doors. Such a fault lies with the driver, not with the car, and eventually the driver learns—or so we hope. The automobile needs a driver; and pictures of it, descriptions of it, even though with a microscope, may be data—but not science.

This innocence of the principles of scientific methodology is more insidious than appears at first glance. It is futile, for example, in an hour's discussion, in a symposium or even in lengthy exchanges of correspondence, to try to teach the average adult the equivalent of what a young active unbiased student is able to acquire in an entire college course which is itself unusual in its intellectual severity. Until such adults, however, are willing to settle down and really think along unaccustomed channels, they may continue to thwart the development of American Plant Ecology. To speak more concretely, the traditional ecologic theories were not proposed and tentatively accepted, and verification was not attempted by methods of logical analysis. They were quickly accepted as "fact" in the early 1900's. Consequently, to get those traditions reevaluated at this time is like trying to indict Truth herself. It will require much extra effort in the way of disassociating bias from analysis. Unfortunately, these four ecology texts show no tendency to appraise concepts. Rather, they avoid all "controversy" and speak only of "real

fundamentals," each according to his own flag—the fertile soil of nationalist science. There is hardly any awareness of concepts as such, but only of that "empirical reality" of the layman and the 19th century naturalists. We find unheeded J. B. Conant's words (1947: 13) that "there must be constant critical appraisal of the progress of science and in particular of scientific concepts and operations." This slight is unfortunate, for in the study of plant communities there is apparent on all sides an urgent need for a basic conceptual reformulation to bring about newer and greater understanding.

One feature of the contemporary fad for ecologic "experimentation" to obtain "absolute data" for the vaunted "quantitative approach" has been the strangulation of what might be referred to as the interpretational method of science. Even the barest acquaintance with the various fields of geology would indicate the tremendous importance that inferential reasoning has played in interpreting the phenomena of this planet. The advances and recessions of the Pleistocene glaciers have not had to be seen and felt and measured to be accepted. We see their evidences in moraines and a host of other surface features. The buckling of mountain ranges is not doubted. The dip of sedimentary strata is evidence. It would almost appear that American ecologists have a pathic fear of using their minds, for the possibility of making an error. Perhaps there is a greater fear of some day having to *change* their minds, always a difficult procedure for the "scientist" who thinks in terms of one truth and one reality. Let it be said however that the inferential reasoning involved in the interpretational method may be one of the most powerful tools in the advance of the science.

Environmentalism is said by some to be the better name for what we now call American Ecology. It has been proclaimed by several investigators that if we could understand thoroughly and completely the nature of the environment, then we would understand all the phenomena of vegetation. The field of psychology (the early history of which seems to parallel present ecology in many ways that are highly instructive) long ago passed out of this stage. I can recall the days when arguments were loud and lusty as to whether environment or inheritance made us what we are. The arguments spread out of the cloistered halls, into the streets, to the stage, the screen and the pulpit. Today we smile at those discussions of yesteryear. There is still ample room for the study of environment in human psychology, but it can no more walk alone as an independent self-sufficient science than can a circus clown walk on one stilt. And yet the study of American vegetation continues to worship at the altar of Oikos. It might be well if a group of fanatics would "reveal a new truth": that vegetation is the sole result of the inherited characteristics of the plants, and that if we understand everything about the inheritance, then we would understand vegetation. The pendulum might move from its present extreme position.

The idea of causation in ecology is closely related to its environmentalism. The *principle of causality* is one of the trickiest in the history of human thought. Whether it is the aspirin that stops our headache, the fire that "causes" the pine barrens, or the forces that affect the constituents of the atom, the problem is not one that can be solved with the flip of a finger. In complete obliviousness of the thought given to this subject by master minds of the past, American ecologists blandly established their cardinal credo: that the cause of vegetation lies in the environment. We have dug for data to support this assumption for 50 years. The data are valuable, and will remain valuable. More such data are needed. But in other sciences, the search for simple single "causes" rather than relationships, has been considered a rather unsophisticated emotional urge, rather than a relatively mature approach to scientific research and

to an understanding of the world about us. Even more (Neess 1950: 233), "it might almost be said that the concept of causality itself is a sort of philosophic dodge, a symbol without a referent, a semantic chimaera that has seated itself so firmly in our intellectual tradition that it can now be dislodged only with great difficulty."

Lack of circumscription of subject matter, its limited methodology, environmentalism and causationism have combined to mold American Ecology into its first fifty years of history—interesting and instructive years. Of the four books discussed above, three completely ignore the history of ecology, the fourth (Oosting's) scans the pre-1900 history. And yet the post-1900 history, close as we are to it, assumes a pattern that is instructive as well as alarming. Contrary to the history of many firmly grounded sciences, we do not find in ecology a clear-cut understanding of the problem to be investigated. We do not find a subsequent amassing of impartial observations, unbiased descriptions, clearly logical classifications. We do not find hypotheses proposed, concepts suggested, theories established, all retained *as* hypotheses, concepts, theories, and their statuses altered as soon as conflicting data demanded a reconsideration. Instead, we find—as in the earlier stages of psychology, and as in revealed religions—a brilliant and elaborate superstructure raised not as hypothesis but as "established fact." Disciples were won and hypnotized by its dogma and ritual. They spread to the four corners of the country, preaching its gospel, flaunting its trappings, but only seldom retaining the core of soundness. Thus we find publication after publication giving us elaborate successional diagrams, identifying every kind of climax in the area. How often I sigh when reading them, wishing I knew what the vegetation *is*, not what it *should be* according to the creed.

This characteristic of American ecology has been accentuated by the high degree of *isolationism* under which it has evolved, and is still evolving. In part, this is because of the fact that Americans show a strong resistance to reading a foreign tongue. Our language requirements for a Ph.D. hardly alter this trait. Science has always boasted of its internationalism. With the present swing to "one world," or at least two worlds, it seems a double disaster that American Ecology should be unwilling to avail itself of the excellent contributions of Scandinavia, Germany, France, and other countries. And yet reading a foreign language cannot be the only factor involved. For example, the British Empire literature on vegetation is extensive and has developed along extremely rational and satisfactory lines, from which we could learn much. And yet it seems to have had no impact on American thought. Braun-Blanquet's text has been in an English edition for 18 years, and yet I find almost no comprehension of the features (I do not refer to acceptance of the features) which distinguish the thought of this volume. It is true that we have adopted from Europe the concepts of the structure of plant communities, but this is not great credit, for these concepts replaced a near vacuum in that phase of our own science. Other features of Braun-Blanquet's Montpellier school seem to be so completely overlooked that one wonders whether there has not been a tremendous amount of psychologic resistance to new ideas, even if appearing in our own English language. The most amusing, and yet serious, example of this, is the adoption in one textbook (Oosting's) of a unique definition of "plant sociology" which is so totally incongruous with all European usage, so etymologically unreasonable, so incompatible with the title of Braun-Blanquet's book that we have in English and with the table of contents of that book, that we are forced to trace its origin to a matter either of carelessness or closed-mindedness.

Furthermore, our resistance to new ideas does not seem to be limited to non-American ideas, even if in our language. In 1948 appeared J. Kittredge's "Forest influences," the first organization in book form of that important ecologic field concerned with the effects of vegetation upon its environment (the reciprocal of what ecologists have concerned themselves with, despite their definition of ecology as the *inter*relations of plants and environment). The word influences does not appear in any index of the four texts here discussed. The subject is not recognized in a single separate heading in any of the books; and, although in each volume there could undoubtedly be found isolated data that reveal influences (especially the "reactions" of Clementsian terminology), such material bears little if any relation to the huge literature that Kittredge organizes in this volume.

This picture of American Ecology is based on the major lines of thought as expressed in the four recent texts. It leaves some of us with an inescapable sense of insufficiency, of a problem, even as Galileo felt about Aristotelian physics. It would be unjust however not to mention certain trends in these first 50 years which cannot be evaluated by the attention that has been paid to them. Borrowing from our knowledge of the history of other sciences, we look for men who may have, intentionally or otherwise, hit upon Baconian inductive methods of observation, description and classification—and stopped there. We find them. Thomas H. Kearney is one, whose empirical descriptions of natural vegetation were appearing at the same time as the first of the Nebraska and Chicago schools. Two other figures assume a considerable stature through the half-century: Roland M. Harper and John W. Harshberger. The voluminous publications of these controversial figures have long been the object of scorn and ridicule. Their "car-window botanizing" and undigested compendia have been held up to generations of students as examples of what not to do. Yet I dare say that a few of the castigators will sneak a look at their papers if they wish to get an overall picture of what the vegetation of an area *is*, rather than what the successions and climax theoretically are. Harshberger was chosen to write the North American volume for "Die Vegetation der Erde," a choice that rankled in many a jealous bosom, and that broke out in vituperative reviews once the book was off the press (1911). Perhaps those German editors had found that formal American Ecology was intelligible only to itself. I do not for one minute wish to imply that Harper and Harshberger represent models of scientific progress. Their work is still too close to us to view it objectively. They come nearest however to a type of scientific activity which American Ecology seems to have passed by. As stated by Northrop (1947: 37), ". . . if one proceeds immediately to the deductively formulated type of scientific theory . . . [as that of Clements], before one has passed through the natural history type of science [as that of Harshberger] with its inductive Baconian method . . . , the result inevitably is immature, half-baked, dogmatic, and for the most part worthless theory." Nowhere else in his book does Northrop speak so strongly.

From an entirely different point of view, H. A. Gleason occupies his own niche in this half-century. In 1926 and 1927 appeared two papers in which he dared to question the sacrosanct status of established ecologic "fact," and to offer as an alternative what he called "the individualistic concept" of the plant community, a concept which recognized the community as existing at a relatively low degree of holistic integration. He presented his opinion solely as a concept, to be weighed against the opposing highly integrated "individual-organism concept." The weight of the opposition, however, against this presumptuous iconoclast was so powerful that it is only in the last few years that his ideas have been gaining

credence. Today, with the much enlarged vistas that holism affords, we can evaluate Gleason's contribution as anticipating that philosophic approach.

Another one-man trend is the trail being blazed by Stanley A. Cain. In the 1930's, Cain was the Peck's Bad Boy of ecologists, and I recall distinctly his being used as an example of what not to follow. It is true that Cain's pendulum has swung widely and rapidly—at least evidence of growth and activity, not intellectual somnolence. The contributions to vegetational thought that Cain has raised over a long period of years are barely evident in the texts here reviewed, and the eventual impacts of his publications can hardly be told at this time.

An extremely interesting rebirth of Baconian inductive science may possibly be taking place these days in Wisconsin. Norman C. Fassett, John T. Curtis and Grant Cottam and their students have been turning out a series of research publications which are remarkable for being devoid of conventional dogma, and for being precise and thorough in their accumulations of empirical material, obtained by contemporary methods of sampling, analyzed statistically without bias, evaluated with care, and with hypotheses and theories presented as they should be in the light of the inferential reasoning on which they are grounded. It was probably coincidence which brought these men together, but it is to be hoped that their work may continue through these primary empirical stages, and on into the much more unusual intellectual maturity of a full-fledged science. At present their work seems one of the brighter glows on the horizon of American vegetation although already with a glimmer of rising too quickly to the blinding glare of premature deduction.

Looking again to the future, we find some faint indications revolving around the broad idea of *vegetation.* Although the term and the concept are well established throughout all Europe, they have not spread to the United States for the simple reason that most Americans do not read that literature. There are still some in this country, for example, who believe that the "science of vegetation" and "ecology" are synonyms. Two of our workers long ago recognized and adopted the distinction between flora and vegetation, Harshberger and Harper, with apparently no effect on other Americans. Oosting (p. 308) does mention "floristic [and] vegetational" approaches, but one strongly suspects that these words were copied verbatim from a reference without critical intent. McDougall and Daubenmire imply no comprehension of the voluminous literature using these concepts. Clements' text is most significantly titled "Dynamics of Vegetation," even though the first sentences of both preface and first chapter refer to "Dynamic Ecology." One wonders if it is the editors who were responsible for the title of the book. And now Buell (1950) in his recent review of Polunin's "Botany of the Canadian Eastern Arctic," sees fit to open his review with " 'The *flora* of an area is the sum total of different 'kinds' of plants inhabiting it, no matter whether they are scarce or plentiful. The *vegetation,* on the other hand, is concerned largely with the question of relative abundance, being the total 'display' that the plants make collectively. Their *ecology* is their relationship to environment. . . .' " Considering the fact that these are internationally standard usages for these words, it is interesting to conjecture why most Americans continue to resist these concepts, by ignoring them, just as if they did not understand them.

Dissatisfaction with conventional ecologic treatments of vegetation, and strong impacts of new ideas are being brought to bear from outside the fold. The foresters and soil conservationists are contributing a wealth of data in the field of "influences." Among the taxonomists are F. R. Fosberg and his unpublished Pacific islands vegetation research. From the plant geographers, W. H. Camp is a leader among

the tradition-destroyers who have killed our simple species that left the Ark, and thus have made our communities far more complex. Genetics has contributed Edgar Anderson (1948); anthropology, George F. Carter (1950); geography, Carl O. Sauer (1950)—to mention but a few whose ideas when amalgamated will help form the matrix of a broader science of vegetation. From another direction, Walter P. Taylor, Victor E. Shelford and others are giving us new and valuable outlooks upon the plant-animal community.

It is in the *concept of holism* that we find rumblings of readjustment. The "holism" of J. C. Smuts (1926), the "emergent evolution of C. L. Morgan (1922), and the "levels of integration" of the zoologists (Redfield 1942) may best be considered as different aspects of the same idea. As the concept pertains to vegetation, it is discussed in an earlier paper (Egler 1942). Holism is an intellectual tool which draws into relationship a vast number of hitherto irreconcilable and unadjustable phenomena. Unfortunately the word "organism" is used both by those who are farthest removed from holistic thought, and by those who grasp holism. For example, when we say that a plant community a is entirely like an individual organism b which is born, lives and dies, we are not holistic in any sense of the term. We are merely equating an unknown phenomenon (the plant community), with a known phenomenon (the individual-organism), and giving it the characteristics of the known phenomenon (*i.e.*, $a = b$). Such a procedure is common experience. We try to describe a tropical avocado x to a north European, and describe it in terms of a pear y. Since, however, there is a slight difference, we qualify it as, *e.g.*, an alligator pear y^{modified}, which does make it different, but only in respect to those qualities embraced in the word alligator (*i.e.*, $x = y^{\text{modified}}$). The terms "quasi-organism" and "complex organism" are concepts of this kind. Our point of reference is still the individual-organism. *This is not holism.* Holism does not equate a and b (to continue the algebraic analogy) but presents the entirely new concept H, for which a and b are two of many possible examples, differing in their levels of integration.

An awareness of holism is beginning to appear in the ecologic literature, even if it is merely a lip obeisance. The word is included in Clements' 44-year-awaited glossary (p. 284) but with a definition from the pen of a humanitarian and mystic rather than of an objective scientist. Holism here is "The principle which works up the raw material or unorganized energy units of the world, utilizes, assimilates and organizes them; endows them with specific structure, character and individuality, and finally with personality, and creates beauty, truth and value from them. The concept of holism, and the whole, is as nearly as possible a replica of nature's observed process." This definition gives an absolutely erroneous understanding of holism as applicable to plant communities. On page 1, Clements repeats a valid dictum of holism, ". . . [the community] is a unified mechanism in which the whole is greater than the sum of its parts and hence it constitutes a new kind of organic being with novel properties." But then follows the old cliché: "Plant communities arise, grow, attain old age and die . . . ," thus *identifying* the community with an individual-organism ($a = b$). Later (p. 130) Clements writes that "in the light of . . . the application of the twin concepts of climax and complex organism . . . and the strong support brought to them by the rise of emergent evolution and holism . . . , the characterization of the climax as given in *Plant Succession* in 1916, still appears to be both complete and accurate. [That is,] 'The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures and dies . . . The life history is . . . comparable . . . with the life-history of an individual plant.' " These

statements prove that Clements read the literature on holism. They also prove that he jumped to the self-satisfying conclusion that since he used the *word* "organism," and the holists use the *word* "organism," both meant the same thing. Alas, no. There appears no doubt that Clements died without having grasped the significance of the *concept* of holism.

Clements is by no means the only one who is certain that he grasped the significance of holism and the various "organisms," and yet has missed the idea totally and completely. The problem bears all the humorous but deep discouragements of the man who is trying to "show" the live elephant to the blind men. More than once, in conversations with colleagues, I have been certain I have succeeded in getting the idea across, only to have my confreres end up with the shattering comment, expressive of total failure to grasp the issue, "I agree with everything you say—but I don't see how you can call a plant community an organism, for an organism dies, and a plant community doesn't. At that stage, nothing more need be said.

Oosting makes no mention of holism. In several places in the volume he expresses dissatisfaction with the results of single-factor interpretations, because of their many interactions; but he always falls back with the excuse that the "complexity prohibits consideration of it as a whole" (p. 75).

McDougall does not refer to holism: he adopts completely the Clementsian stand that (p. 150) "as an individual the plant community is born, it grows and develops, it matures, reproduces, and may finally die like any other organic individual." This thesis is elaborated into a page and a half of comparisons. Again, we see a mental process of "identify," *not* an awareness of a totally new concept. Mention should be made here that the concept of symbiosis is a partial approach to the more advanced idea of holism. Symbiosis is concerned with two units that are interacting with each other, and with our attention focussed *separately* on those two units. It is as if we were watching Junior and Sonny on a see-saw: we are concerned directly with the two youngsters, their reactions, and whether or not each stays on. If we switch our view to the whirling May-pole, with strangers' children at the ends of the streamers, and if we are concerned with the whirling system as a whole without reference to any one child, then we are considering it as a holistic unit. Symbiosis has its advantages in scientific investigations, but it is not to be considered as the equivalent of, or a substitution for, holism.

Daubenmire assures us in the preface (xi) that "the most important contribution of autecology as a discipline is to inculcate the holistic outlook," and then follows up that statement with an entire text book on a non-holistic factored environment. Only at the very end does he pull together the loose factors by "interactions." Again, this is *not* holism. In the face of all these misfires on the nature of holism, and on the claim of the holists that one who does not understand the concept of emergent evolution as applied to plant communities is hardly suited to handle the subject, a problem very obviously remains unresolved.

Postlude

In closing this commentary on American Plant Ecology, it should be emphasized that the consideration has been primarily with national trends, and with individuals only as the voices of the times. If it is to be thought of as an indictment, then it is an indictment of the era—but not of individuals. I have been accused, in this manuscript, both of being holier-than-thou, and of being satanic. With either accusation, I plead that to be both forceful and modest at the same time is a difficult task. If I appear to claim that I can see farther and from greater heights than some others, it is only—to use Newton's oft-quoted analogy—that those few cubits of stature have been attained by climbing on the backs of giants. The giants

are there for others to climb upon, even though the shoulders may bear us ungraciously.

It would be unjust not to add a statement that the conditions mirrored in the preceding pages are but reflections of phenomena that concern the physiologist, the psychologist and the human sociologist, not the botanist. The resistance to change, the "closed-mindedness," the "die-hard" qualities, the inability of most men past middle age to question the traditional, to welcome innovations or to grasp new ideas, are all recognized qualities that create the conservative forces in human civilization. The resistance and resentment toward each new advance in the history of art also is paralleled by the treatment of Copernicus, Galileo, Pasteur and a host of other scientists. It is not the conservatives of today for whom the American Ecology of 1900–1950 poses a problem that challenges our ingenuity.

To this problem we have to add conditions peculiar to our contemporary society. Our individual lives are prolonged, but not necessarily the elasticity of our minds. We are university-bred scientists, but rarely are we subjected to a formal course in scientific methodology, or in the philosophy of science. We must admit the extraordinary degree of specialization to which our rapidly enlarging bounds of knowledge are driving us. The versatility of Cellini and Michelangelo belong to an age gone by. A man who claims today to be a "general botanist" is considered scatter-brained. To be an ecologist alone is now more than a one-man task. A few decades ago one could hold a full teaching schedule, keep a complete up-to-date card catalogue of the literature being published, read that literature, carry on one's own research, and write a textbook. The overwhelming increase in the student enrollment in our universities has added murderous loads to many professorships. The flood of technical literature that flows ever more abundantly from the press has sent many scurrying to abstract journals. Magazines of the order of Botanical Review are all too few. One can carry on his own research only by short-circuiting other professional and social obligations. Our superiors keep urging us to publish professional papers. And in turn, we worship what we call "research activity"—which seems to comprise the accumulation of vast quantities of "original" data. Such accumulations may require some original thinking in their early stages; but thereafter, a robot-like repetition, on a par with that of a technician or a practitioner, suffices. Furthermore, this activity makes a greater impression if it is released in several publications, the more the better, even if in part they repeat each other. Of the problems of future bibliographers, we are not concerned. With all this, we have no time to think, even had we the ability to think. In any event, we have not yet adjusted to this new social phenomenon of extreme specialization, and are neither willing nor able to accept a smaller role in the academic firmament than what the same effort would have given us 25 years ago. The result is seen in the state of American Plant Ecology, which cannot get over the hump of its own voluminous literature in order to help establish a world science, and cannot apportion its own subject matter for cooperative coverage by various individuals at several hierarchic levels. The solution of the problem lies in the next half century. Even though we are all unavoidably entangled in the inexorable processes of history, it is to be hoped that a vigorous individualism will somewhere arise. Though it may grate on the sensibilities of the established order, it may blaze the necessary trail toward new horizons.

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NOTE. In presenting here my ideas on Doctor Egler's thought-provoking essay, I am following a precedent established in the earliest issues of this journal by Barrington Moore, its first editor. I do this without any possibility of its becoming a habit since this is the next to last issue of ECOLOGY for which I am responsible. Doctor Egler is perhaps the only one among us today with the intestinal fortitude and inclination to prepare an essay so critical. He raises many issues that need to be thought through by each one of us if we are to present students, scientific colleagues, and laymen with an intelligent and intelligible picture of what ecology is, what it is good for, and whither it is bound. In this reexamination of the structural soundness in foundation of the household which we claim to be the object of our study, we ought not to forget that it is the *ecosystem* in which organisms and environment are considered together as a unified whole, that is the ultimate goal of ecological study. There are many levels of integration at which the researcher in ecology may logically focus his attention. A great deal of work is needed at each level if a sound foundation is to be constructed upon which ecology at its highest integrative level with focus of attention on the interplay of materials and energy in the system as a whole is ultimately to be built.

Doctor Egler is by profession a "vegetation scientist" with focus of attention at an intermediate level. In an earlier publication (1942) he recognized the eco-

system concept as "intellectually more acceptable" than any other, yet he has avoided it for his reason that "the natural phenomena appear at present too complicated for study and development as a separate science." Ecologists have not been inclined in the past to shrink from complexity; let us show our critics a willingness to follow the lead of such pioneers as Raymond Lindeman in daring to tackle the ecosystem as a whole!

Doctor Egler has here shown that ecologists are criticized for diffuseness of purpose and lack of clarity in defining the boundaries of ecology. This seems to me a criticism of the very character that is making ecology a useful and great science. Ecology should pride itself in being a science which encourages the worker to consider within the purview of his study anything and everything which affects or is affected by living organisms, from the smallest parcel of material-energy to the vast expanse of the universe. This character must be vigilantly guarded from those who would divert our path from our ultimate goal, the study of the ecosystem.

Finally, I would register my displeasure at Doctor Egler's implication of a *national* ecology even in the form practiced in these United States. Although we may not adequately acknowledge in our textbooks, the debt of information and method derived from our neighbors across the seas, that debt exists to a degree that renders the designation "American Ecology" unjustified, and contrary to the basic precepts of any science.

Doctor Egler's avowed intent in preparing this critique of plant ecology and ecologists was to provoke reexamination of the foundations of ecology. Everyone will agree that this is a worthy purpose and that scrutiny and analysis of ecology by ecologists is a sign of healthy growth toward maturity, and a promise of ultimate attainment of stature that will command the respect of all. I present these thoughts as my small contribution to the reexamination process stimulated by Doctor Egler's essay. May there be many other expressions of view on these matters!

DONALD B. LAWRENCE
BOTANICAL EDITOR

THE DIURNAL PERIODICITY OF *DROSOPHILA PSEUDOOBSCURA* IN SOUTHERN CALIFORNIA

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The advantages of *Drosophila* which have made it ideal for many kinds of genetic research are combined in *Drosophila pseudoobscura* with the advantage of an ecology which limits it to areas comparatively undisturbed by man. Dobzhansky has made use of this combination in his extensive studies of the genetics of natural populations. However, the natural history of this species is relatively unknown and apparently quite complex. Difficulties in the interpretation of genetic phenomena therefore arise. Until very recently *D. pseudoobscura* was known in nature only from adults captured in collecting cups, and even now very little is known about ovipositing, the larval habitat, pupation sites, and breeding habits under natural conditions. The discovery and description of these and other ecological relationships is necessary in order that the genetic phenomena which have been observed can be fully understood. One of these relationships is the diurnal periodicity of locomotor activity which was described by Dobzhansky and Epling (1944). The present paper is concerned with the reaction of adult flies to the major physical factors of the environment, so far as these reactions affect the diurnal periodicity.

METHOD OF STUDY

Wild yeasts are the principal food for both the larval and adult stages, and the flies are abundantly attracted by fermenting fruit. In this investigation a common method of capture was used. A series of cups containing fermenting banana was placed on the ground in the collecting area. These cups were then visited at regular intervals and the flies which had been attracted to the bait were captured by inverting a funnel over the cup and allowing the flies to make their way up into a vial. With this method practically all the flies that visited the cups were captured and records of their appearance at various times of the day were obtained. Although the sudden introduction of an abundant food supply into the collection area may induce a somewhat artificial response, it is probable that the inherent response of the flies to the physical factors of the environment is not greatly modified.

Temperature, humidity, and light are the factors which have been considered as possibly having some limiting effect on the periods during which the flies visit the food cups. These factors are interdependent, but they differ in their daily range of variation, and the reaction of the flies to each is quite different. Temperature and relative humidity were measured with an aspirating psychrometer which was held one to two feet above the collecting cup. The light intensity was obtained by placing the sensitive element of a portable light meter (Weston Illumination Meter, model 756) in the same position. These values are only approximate because the light intensity varies from spot to spot. However, care was taken to always expose the element in the same manner and direction. The readings of all three factors were made directly after the flies were captured in the particular cup.

SEASONAL CYCLE

The range of *D. pseudoobscura* extends from British Columbia to Guatemala, and from the Pacific Coast to the eastern slope of the Rocky Mountains. Although there is a considerable range of climate within this area, much of it is of an arid or semi-arid nature. Precipitation occurs briefly during one season and is followed by low

rainfall or drought. The seasons of maximum rainfall and temperature do not necessarily correspond, but vary from region to region. Precipitation-evaporation ratios by months are shown in Dobzhansky and Epling (1944, p. 157). The optimum combinations of rainfall and temperature for an increase in population density vary from region to region. The result is that the fly populations reach their maxima at different seasons in different places. There is reason now to believe that this may also be in part the effect of temperature and rainfall on the wild yeasts on which the flies feed.

The seasonal maxima of population size may occur at different times at stations short distances apart if differences of elevation modify the climate. The seasonal maximum occurs in March and April at Andreas Canyon, which is at the foot of the San Jacinto Mountains on the margin of the Colorado Desert, but in June and July at an elevation of 5,000–6,000 feet at Keen Camp and Idyllwild. The range of relative humidity and temperature are similar at the two localities when the flies are active, as suggested by Figure 2. The total number of flies which appear at the cups is accordingly determined by their abundance at a given season. The numbers that appear at different times of day are determined by the factors which control the diurnal cycle.

The Normal Diurnal Cycle

The flies appear in greatest numbers in the morning and in the late afternoon. The periods during which they visit the cups are generally short. The peaks of activity occur at approximately the same time relative to sunset or sunrise regardless of the station; however, both the peaks of activity and the activity periods

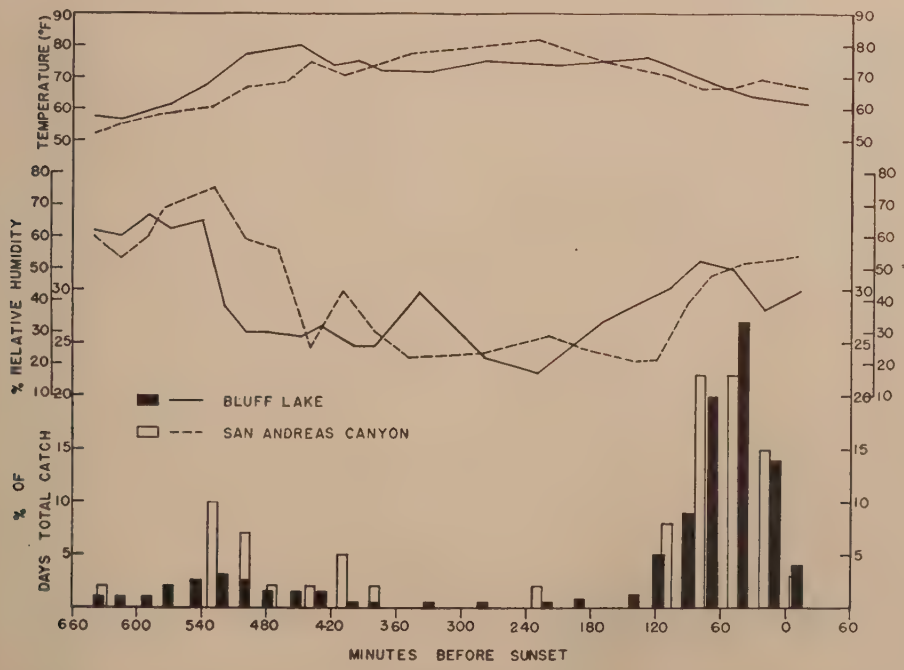

Fig. 1. The diurnal behavior of *Drosophila pseudoobscura* at Bluff Lake in the San Bernardino Mts. on August 17, and at Andreas Canyon on the edge of the Colorado Desert on November 8, with the corresponding conditions of temperature and relative humidity. The Bluff Lake data are equated to the day length of November 8.

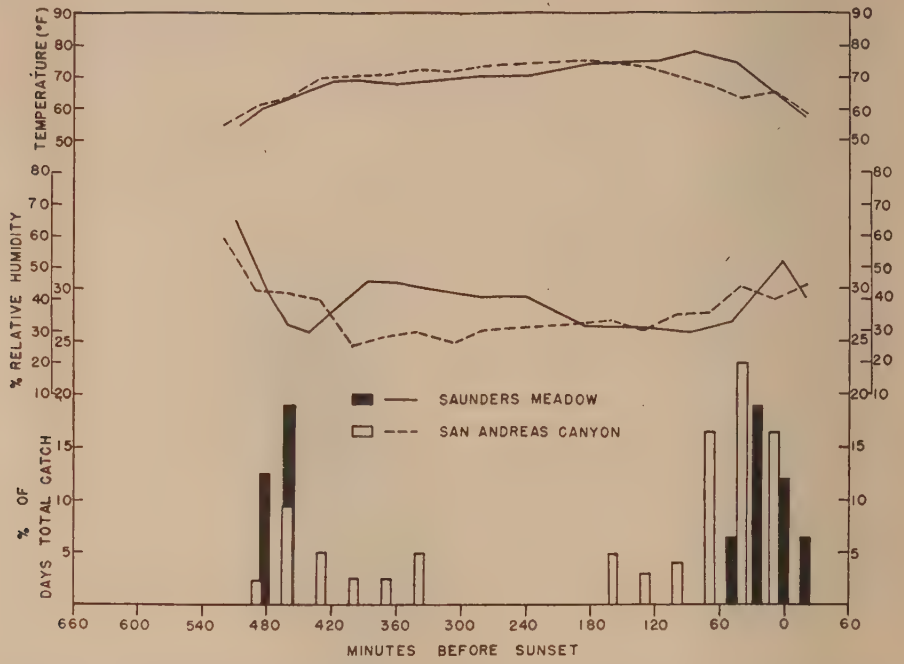

FIG. 2. A comparison of the activity at Andreas Canyon on December 7, near the winter solstice, and at Saunders Meadow in the San Jacinto Mts. on June 25, near the summer solstice. The Saunders Meadow data are equated to the day length of December 7.

may be modified by factors which will be discussed later. The flies disappear from the cups at dusk and have never been captured at night. Figure 1 illustrates the cycle. It compares the activity during collections made at Bluff Lake in the San Bernardino Mountains on August 17, 1942, and at Andreas Canyon on November 8, 1941. These localities are roughly 30 miles apart; the former lies at an elevation of about 7,300 feet and is in the upper level of the montane forest, the latter is near sea level on the margin of the Colorado Desert. Both sets of data are equated to the same day length, using November 8 as the base. The mean trends of temperature and relative humidity are very similar. The morning peak of activity at both stations occurred during rising temperature, increasing light, and falling relative humidity. The opposite conditions existed during the evening peak of activity.

Seasonal variation of the cycle

Figure 2 compares the activity during collections made at Andreas Canyon on December 7, 1941, near the winter solstice, and at Saunders Meadow in the San Jacinto Mountains on June 25, 1942, near the summer solstice. The latter site is in the montane forest at an elevation of about 5,000 feet. These curves are also equated to the same length of day, using December 7 as the base. Their relation is again very similar to the curves of Figure 1, except that the Saunders Meadow activity was limited to definite and relatively short morning and evening periods. The Bluff Lake collection (Fig. 1) is atypical of summer collections, as will appear later, since it was made on a cloudy day. Even so, the trends of temperature and humidity for it are very similar to those of Saunders Meadow, with the latter being somewhat warmer and drier.

Local variation in the cycle

The peaks of activity may vary more during the same evening at stations adjacent to each other, but existing under different conditions, than between widely separated stations at different times of the year. Figure 3 compares the curves of activity on December 7, 1941 for the Andreas Canyon station and for a station on an alluvial fan about 200 yards distant. The canyon station is along a stream bordered by alder, willow, and palm, and is shaded late in the day by the mountains. The station on the alluvial fan is in the *Larrea* vegetation, an open stand of small-leaved bushes characteristic of the desert. It is on the margin of the broad canyon of which Andreas Canyon is a branch. The curves indicate that the total morning activity on the fan was considerably less and that it began earlier and stopped earlier than the activity in the canyon. The conditions of temperature were essentially the same during both periods of activity, ranging from about 55–72° F. The conditions of humidity were similar, differing mainly in the fact that the relative humidity of the fan remained essentially the same all day, while that of the canyon dropped somewhat in the morning and rose in the evening.

The humidity relationship itself was apparently not a factor limiting activity on the fan. Either the rise in temperature or the difference in light intensity would seem to have been more effective. However, peaks of activity have been recorded at 85–89° F. (Fig. 7), and it would seem that temperature was not responsible for the difference. The light intensity was measured only in the canyon, and indi-

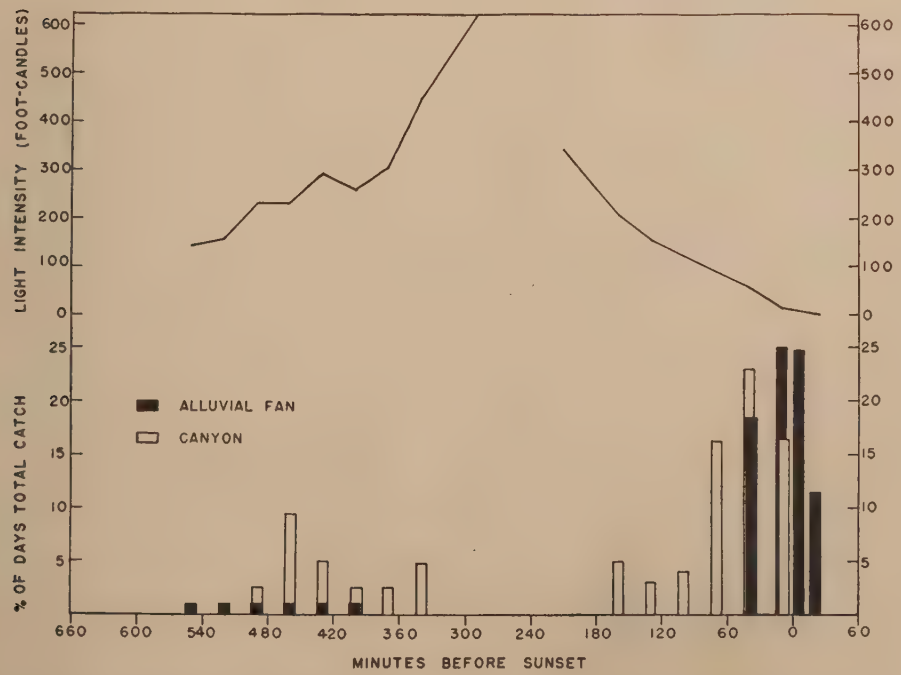

FIG. 3. A comparison of activity at the Andreas Canyon station and at a station on the alluvial fan approximately 200 yards distant on December 7. The light intensity curve was obtained for the canyon station only. Temperature and relative humidity did not vary significantly between the two stations.

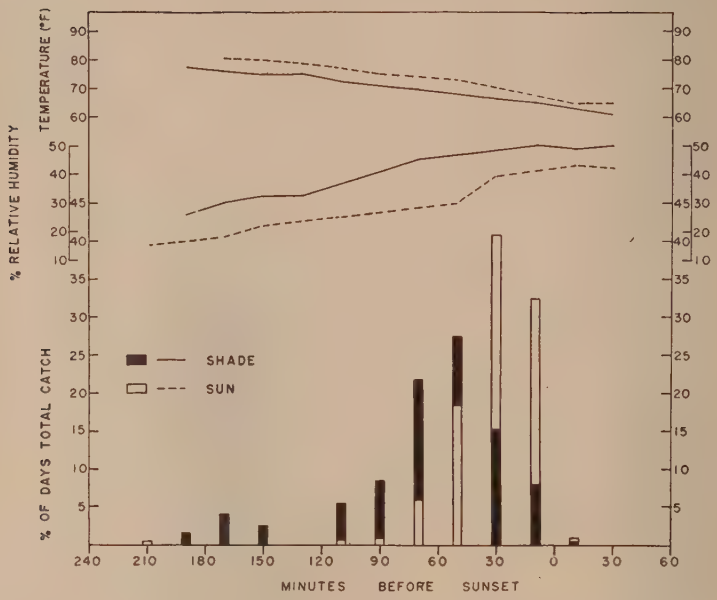

FIG. 4. A comparison of activity, temperature, and relative humidity on the shaded and sunny slopes of a ravine at Saunders Meadow on July 30, during the period of evening activity.

cated that the significant activity there took place below an intensity of 400 f.c. The peak of evening activity for the fan, which was in sunshine longer, followed that of the canyon by about 30 minutes at which time the canyon was in deep shade. Figure 4 provides a similar contrast for two stations at Saunders Meadow on July 30 when the data were gathered on the shaded and sunny slopes of a ravine. The conditions of temperature and humidity were essentially the same at the time of arrival of the flies in both instances and did not differ significantly throughout the period. On the sunny slope the arrival of the flies and the peak of activity were later, just as on the more open fan at Andreas. Intensity of light would seem to have been the limiting factor in both cases.

Variations due to clouds and rain

The effect of clouds and rain may greatly modify the curve of activity. Mention has already been made of the continuous activity at Bluff Lake (Fig. 1). This site was in a fairly well shaded forest and the day on which the data were gathered was cloudy. No other data are available for this locality but by repeated visits a day could probably be found with essentially the same conditions of temperature and humidity but no clouds. Under these conditions experience indicates that the peaks of activity would be (like those of Saunders Meadow) more sharply confined to the morning and evening periods as the result of the increase in light intensity during midday.

These observations are borne out by data gathered on two rainy days, July 6, 1950, and July 22, 1948, on an experimental plot at Mountain Center, near the Keen Camp locality (Figs. 5, 6). On both days the temperature remained essentially the same throughout the periods indicated. Those of July 22 were recorded on a hygrothermograph about 12 feet above the ground in the crown of an oak tree; those of July 6 were taken

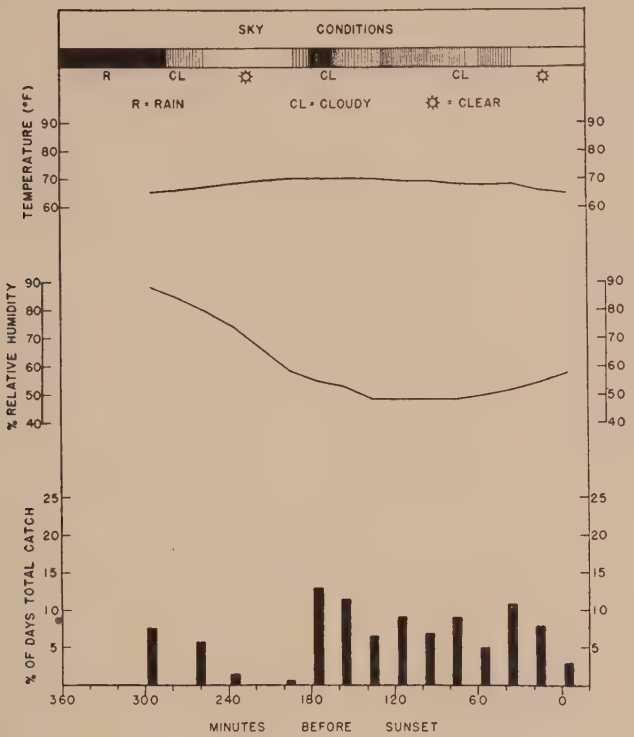

FIG. 5. Activity, relative humidity, temperature, and sky conditions during a rainy day at Mountain Center on July 22.

from a psychrometer near the surface of the ground in an opening shaded from direct sun. The relative humidity varied greatly during the peaks of activity on both days. The first peak of activity on both days followed the rain and occurred at a relative humidity of 80 per cent, while the second peaks followed a period of direct sunshine and occurred at relative humidities of 50 per cent and 65 per cent. This suggests again that neither temperature nor humidity, nor a combination of them is the effective limiting factor. In Figure 7 is shown the period of activity on the same plot at Mountain Center on August 6, 1948. The temperatures were only slightly higher than those of July 6, but the mean relative humidity was 10 per cent as compared to 60 per cent or more on July 6. Similar differences of humidity may occur on successive days, with the temperature remaining fairly constant. Even in such cases the periodicity of the flies is not materially affected.

The conditions of illumination during and after both thunder showers and their relation to activity are of particular interest. The shower on July 22 began about noon, moderate rain fell for two hours and very light rains continued for approximately another hour. The first collection was made about 2 o'clock while the sky was still dark and a light rain was falling. Soon thereafter the rain stopped and the sky cleared shortly before 3 o'clock. Bright sunshine fell on the plot until about 4 o'clock, when clouds again formed. These clouds disappeared shortly before sunset. Although the cups were visited every 20 minutes during the interval of bright sunshine, no flies ap-

peared. They reappeared only after the sky had darkened to an extent which would have given a photometer reading of less than 500 f.-c.

On July 6 the shower began about 10 o'clock, produced heavy rainfall until about 11 o'clock, and lighter rain thereafter. The cups were put out during the lighter rain, and the sky cleared before it was possible to collect the flies (which rapidly disappeared) and make readings of temperature, humidity, and light at the six cups used. However, the flies were abundant during the overcast conditions and those that were captured formed about 15 per cent of the day's total collection for that cup. There followed a short period of bright sunlight, then of increasing cloudiness, and at about 1:30 a shower with a consequent dark sky. This was followed by variable cloudiness and a period of direct bright sunshine. The later afternoon was more or less overcast. During both periods of direct sunlight the flies disappeared completely, as on July 22. The intensity of light during these periods was greater than 500 f.-c. Flies began to arrive at the cups with readings of 300–500 f.-c.

Daily observations at Mountain Center

The correlation of light intensity with activity, despite marked differences in relative humidity, is further illustrated by Figure 7. This graph compares the activity at Andreas Canyon of December 7,

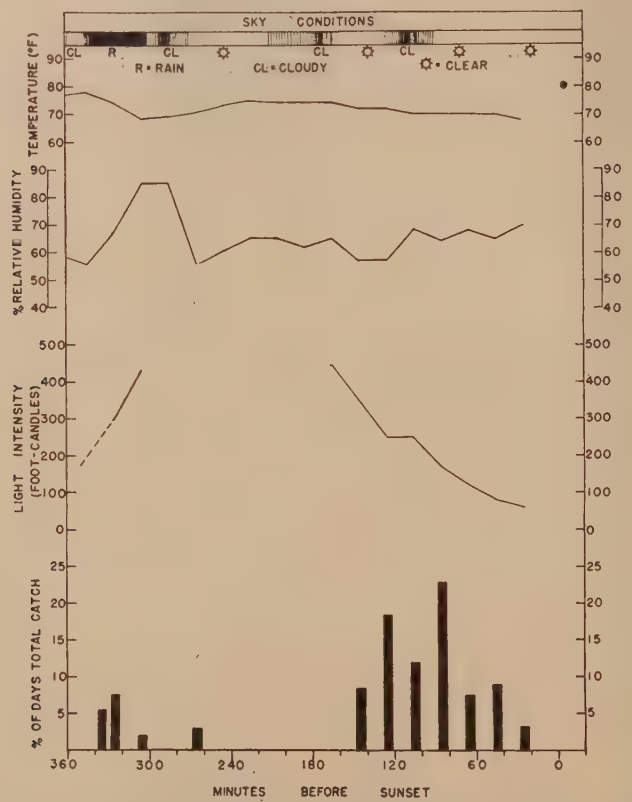

FIG. 6. Activity, light intensity, relative humidity, temperature, and sky conditions during a rainy day at Mountain Center on July 6.

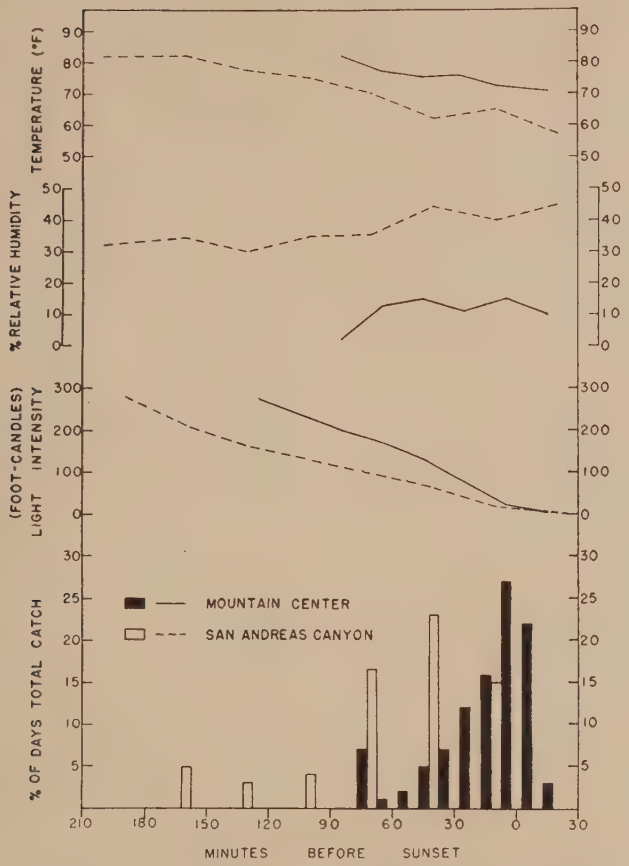

FIG. 7. A comparison of activity, light intensity, relative humidity, and temperature during the evening activity periods at Mountain Center on August 6, and Andreas Canyon on December 7.

1941, and at the Mountain Center plot on August 6, 1948. Although the humidity was very different on the two days and the temperatures differed (but to a less extent), both periods of activity were initiated under about the same conditions of light intensity, between 200 and 300 f.-c. The peaks were reached at less than 100 f.-c.

For several weeks during the summer of 1948 collections were made every 10 minutes during the period of evening activity on the plot at Mountain Center. For these collections 6 cups were arranged in two parallel lines with the distance between cups 50 feet. One line of three cups ran down the more shaded bottom of a wash, while the three remaining cups ran in a parallel line on the more open and sunny slope. The results from these collections are much too bulky to be presented here but confirm the data previously presented. Flies arrived at the three most shaded cups generally 10 to 20 minutes earlier than at the cups in the open, and left the shaded cups usually about 5 minutes earlier. Only occasional individuals were captured when the light intensity was greater than 300 to 400 f.-c., and arrivals at the cups ended with meas-

urements of from 5.0 to 1.0 f.-c. The peaks of activity in the three brighter cups occurred significantly later than in the shaded cups and were usually reached when the light intensity was between approximately 100 and 15 f.-c., with a rough mean of 25 f.-c. The differences of humidity between cups were less than 3 or 4 per cent, and the temperature differences were less than 2° or 3° F. During these collections the flies captured at the three shaded cups outnumbered those captured in the other cups by a ratio of 3 to 1.

Discussion

In their discussion of the ecology of *Drosophila pseudoobscura,* Dobzhansky and Epling (1944) presented a considerable amount of data relevant to diurnal periodicity. They found that variations in relative humidity had very little effect on the activity cycle, and that although the temperature affected the abundance of flies in the collecting cups, it did not affect the periods of activity. Thus they suggested the hypothesis that light intensity was the major controlling factor. This hypothesis was based on observations of the regular cycle in the evening during clear days, and on the upset of the cycle on cloudy days. The report of these investigations did not present any records of the actual light intensities.

Analysis of the combined data show that the flies visit the cups when the temperature is between 50° F. and 90° F. and the light intensity less than 300 to 400 f.-c. and greater than about 1 f.-c. These conditions exist in this region only during the mornings and evenings of clear days and occasionally on cloudy days. Because of the extreme depletion of the populations during the summer and winter months, flies may not appear even though light and temperature conditions are optimal. This depletion of the populations is undoubtedly the result of extreme temperature, or aridity, or both, which affect some stages of the life cycle of the fly, or its food source.

Ecological function of the diurnal cycle of activity

Although much of the area inhabited by these flies is of an arid or semi-arid character, they have no obvious adaptation (except in respect to behavior) to prevent water loss. Lilleland (1938) demonstrated that starved individuals of this species survive much longer (57–93 hours) at 95 per cent relative humidity than they do at 0 per cent relative humidity (38–53 hours) when kept at a temperature of 24° C. Thus water conservation is of great importance under the rigorous conditions of temperature and humidity encountered during midday in summer. The flies are occasionally quite active at humidities as low as 10–20 per cent and temperatures of 85–90° F., but activity under these conditions is rare since the flies are limited by light intensity to the morning and evening periods, or cloudy periods when the temperature and humidity are generally less extreme. It appears, then, that the striking diurnal periodicity of this species is a behavioral adaptation to conditions of temperature and humidity, which functions to prevent desiccation, and that this behavior is evoked and limited by a response to light intensity. Pavan, Dobzhansky, and Burla (1950) found that the activity of Brazilian species is apparently correlated with fluctuations in relative humidity, and that the cycles are much less definite than in *Drosophila pseudoobscura.* Since most of these species are found in the humid tropics the danger of desiccation would not be as extreme.

Nature of the behavioral response

A considerable amount of information is available concerning diurnal rhythms. Some of the information is concerned with physiological rhythms which are usually correlated either with a rhythm of behavior or with a rhythmic fluctuation of environmental conditions. In addition a number of examples of the periodicity of locomotor activity have been described,

and it has been shown that the stimuli which elicit the behavioral responses in these organisms may be quite different. For example, the beetle *Boleototherus cornutus* exhibits a twenty-four hour rhythm of locomotor activity even after being raised in the laboratory from the larval stage under conditions of constant darkness, temperature, and evaporation rate (Park and Kelly 1932). This rhythm is probably metabolically determined and is comparatively independent of natural external stimuli. On the other hand *Ptinus tectus* exhibits a diurnal rhythm of locomotor activity which persists for a few days in constant light and then gradually disappears (Bentley, Gunn, and Ewer 1941). When individuals of this species were raised under constant illumination no activity rhythm was apparent, but a single period of darkness appeared to be sufficient to permit the establishment of a rhythm which then persisted for a few days in constant light. The activity cycle in this species is apparently "primed" by the diurnal cycle of light intensity.

A rhythm has been described in *Drosophila melanogaster* which involves a definite tendency for emergence from the pupal state to occur in the morning (Bremer 1926). The work of Bünning (1935) indicated that this cycle could be altered by changes in lighting but that it persisted for some time under constant illumination or in constant darkness. This also is apparently a metabolic cycle which is conditioned primarily by change in light intensity. The existence of a similar tendency in *Drosophila pseudoobscura,* when it is grown in the laboratory, suggests that the diurnal cycle of activity might be of a similar nature. Two observations indicate, however, that the diurnal response of *D. pseudoobscura* is not endogenous. The first observation is that marked flies which were released at Idyllwild and Keen Camp "fell almost immediately into the diurnal cycle characteristic of the wild flies in the same locality" (Dobzhansky and Epling 1944, p. 33). These flies were laboratory bred, presumably under light conditions quite different from those existing in the natural sites. The second observation is the activity on rainy days as depicted in graphs 5 and 6. The extreme upset of the normal diurnal cycle by changes in light intensity during these periods indicates that it must be a simple response to this stimulus. In respect to environmental control, the behavior observed in *D. pseudoobscura* is probably opposite to that observed in *Boleototherus cornutus.*

Effect of the diurnal cycle on migration

Dobzhansky and Epling (1944, p. 44) state that, "in reasonably uniform two-dimensioned environments the flies move at random rather than follow density gradients. No 'homing instinct' or 'territoriality' is present." The movements are not random, however, insofar as they may be directed by attraction to feeding sites, breeding sites, and shelter. The same authors state further, "If the temperature at the time of the evening maximum of activity of the flies is close to 70° F., the average distance from the starting point traveled by the flies per day is approximately 80 meters. The migration rate grows or diminishes exponentially with changes in temperature." The experiments from which the above value was computed were conducted in June at Keen Camp and Piñon Flat, during the height of the season and in a year when the populations were large.

The temperatures to which the flies are subjected during the activity periods vary from locality to locality because of various topographic, vegetation and climatic relations. For example, the altitude and exposure differences of Piñon Flat and Keen Camp result in quite different seasonal temperatures. Two-year averages for 1949 and 1950 of the mean temperatures during the evening activity periods, computed monthly, for Keen Camp are as follows: April 58° F., May 65° F., June 73° F., and July 76° F. On the basis of the effect of temperature on migration as reported by Dobzhansky and Epling it

can be inferred that little effective movement takes place in April and May. The same means for Piñon Flat are: April 60° F., May 69° F., June 77° F., and July 80° F. If only the effect of temperature is considered the effective migration at this station would be greater each month. However, other factors also affect the migration rate.

The light intensities to which the flies are subjected vary in much the same manner as the temperatures because of differences in vegetation, slope, prevailing sky conditions, and latitude. The light conditions under the canopy of the yellow pine forest at Keen Camp are quite different from the light conditions in the comparatively open piñon-juniper association at Piñon Flat. Because of the greater shading effect of the trees at Keen Camp, activity tends to begin sooner in the afternoon, and consequently to be of a longer duration. With the longer period of flight activity, opportunity exists for a greater mean distance of migration. The light intensity factor therefore tends to increase the rate of dispersal at Keen Camp over that of Piñon Flat, while the temperature factor has the opposite effect.

The amount of effective migration which will take place in a given season is determined by the relationship of the diurnal range of temperature, the diurnal cycle of light intensity, and the population density. In early spring, in Southern California, the morning and evening periods of activity are comparatively long. In March and April on a clear day the flies become active shortly after sunrise (depending on the temperature) and are active until 9 or 10 A.M. Significant activity is resumed at 3:30–4:30 P.M. and continues until shortly before sunset. Since the favorable conditions of light intensity permit the flies to be active during a large part of the day, more opportunity exists for dispersal. However, the low temperatures limit the movements of the flies and thus counteract the otherwise favorable conditions. The populations are expanding during these months and presumably there is an abundant food supply. Under such conditions, flies that move any distance would find favorable conditions for feeding and breeding, and the migration which occurs would tend to be more effective than migration during other periods. However, under these conditions the stimulus which results in the movement of the flies might be reduced because of the abundance of feeding and breeding sites.

In late June or in July activity may last only two hours or less in the morning and an hour or less just before and after sunset. Our data suggest that this extreme restriction of the activity periods is a result of the changed conditions of light. The temperatures during these months are relatively high and are thus conducive to comparatively rapid dispersal, but the restriction of activity by the increased light intensity counteracts the favorable temperature conditions. During these months the populations have either reached their highest density or are decreasing in density, and conditions are unfavorable for the survival of migrant flies in the established populations.

Although more data are obviously needed, the periods during which the maximum effective migration occurs at Keen Camp and Piñon Flat can be estimated by considering the combined effects of temperature, light intensity, and trend of population density. The Piñon Flat population reaches its maximum density in late April and May when the mean monthly temperatures during evening activity are respectively 60° F. and 69° F., and when the activity periods are still relatively long. In March, when the population density is increasing, low temperatures limit the flight activity. In June and July the temperatures are relatively high, but the population density is rapidly decreasing and the activity periods are very short. Thus, at Piñon Flat, the maximum amount of effective migration probably occurs in April and May, even though the population is approaching, or has reached, its maximum

density. The situation at Keen Camp is somewhat different. This population reaches its maximum density in June and early July. The mean monthly temperatures during the evening activity periods are 73° F. and 76° F. respectively, while the activity periods are comparatively restricted. During late May and early June the population density is increasing, the activity periods are still relatively long, and the temperatures are high enough to allow significant migration. Thus the greatest amount of migration probably occurs in this period.

A comparison of the factors affecting dispersal at these two stations indicates that the effective migration at Keen Camp may be greater than that at Piñon Flat. This is the result primarily of two factors: One is the modifying effect of the pine forest at Keen Camp on light intensity; the other is the longer seasonal range of activity, with a later peak of abundance, and with significant dispersal during the period of increase of population density. These effects of temperature, light intensity, and population density on migration in turn affect the degree to which populations within these areas are genetically differentiated. Dobzhansky and Epling (1944, p. 44) conclude that the migration rates determined at Keen Camp and Piñon Flat seem small enough to permit genetic differentiation of populations a "few" miles apart. The frequencies of allelic lethals determined by Dobzhansky, Holz, and Spassky (1942), and by Wright, Dobzhansky, and Hovanitz (1942) indicate significant genetic differences between Keen Camp and Piñon Flat. They also indicate that several populations at Keen Camp 2 to 3 miles apart are not significantly different. However, the stations in the Keen Camp locality that were tested are all situated in a more or less uniform and continuous yellow pine forest, where, as discussed above, the effective seasonal migration may be comparatively large. Had more samples been taken from stations in the more open piñon-juniper association of Piñon Flat it is possible that a significant difference in allelism of lethal genes might have been obtained, especially if the samples had been taken during the early part of the season before any migration had taken place. One factor which might modify this conclusion is the effect of the distribution of feeding and breeding sites on dispersal. Unfortunately very little is known about these sites at the present time.

Within an area of continuous and uniform vegetation, the diurnal and seasonal cycles of temperature, humidity, and light intensity would tend to be uniform, the seasonal fluctuations of population density would tend to be uniform, and the feeding and breeding sites would tend to be more or less uniformly distributed. Since these factors control the movements of the flies, the migration rate would tend to be uniform throughout the area. Under these conditions genetic differentiation would be of a clinal nature, and would be primarily a function of distance. If the vegetation should be of a type which has a high shading effect, the migration rate would be comparatively high, and gene exchange would be facilitated over greater distances. The change of gene frequencies and genetic differentiation would be gradual. If, however, the vegetation should be sparse and open the migration rate would be comparatively low and the change of gene frequencies and genetic differentiation would tend to be more pronounced. In a situation in which areas of vegetation with a high shading effect are separated by areas of open vegetation, the migration rate, and consequently gene exchange, would tend to be greater within the more shaded areas and less in the intervening areas. Such a situation would put a restriction upon genetic exchange between the shaded areas and thus facilitate genetic differentiation of the inhabiting populations.

Summary

On clear, warm days *Drosophila pseudoobscura* exhibits a definite diurnal cycle

which involves early morning and late afternoon periods of activity. The character of this cycle varies with the season, the activity periods being longer and less definite in the early spring months, and shorter and more definite in the late spring, summer, and fall months. The cycle is greatly modified on sufficiently cloudy days.

Variations in relative humidity do not seem to have much effect upon the periodicity, while variations in temperature effect the degree but not the time of activity. The time and duration of the active periods are correlated with definite ranges of light intensity. If a population is of a sufficient density, flight activity occurs when the light intensity is between 300–400 f.-c. and approximately 1 f.-c., and when the temperature is between approximately 50° F. and 90° F. A maximum of activity usually occurs between 100 f.-c. and 15 f.-c. during the late afternoon period of activity. The diurnal periodicity appears to be the result of a behavioral response to light intensity, and it is probably an adaptation which functions to prevent desiccation.

The restrictions placed upon flight activity by the diurnal cycle of light intensity accordingly limit the periods during which dispersal of the flies can occur. The effective seasonal migration in any particular locality will be determined by the interaction of the following factors: the diurnal and seasonal cycles of light intensity, the diurnal and seasonal cycles of temperature, the seasonal cycle of population density, and the seasonal variation in the nature and distribution of feeding and breeding sites. All of these factors are affected by the character of the vegetation.

The amount of effective seasonal migration in any particular area will determine the rate of genetic exchange in that area, and therefore determine the character of the genetic differentiation of the inhabiting populations.

Acknowledgments

Some of the data which have been used in this analysis were referred to by Dobzhansky and Epling (1944) and were obtained either by those authors or by associates whose efforts have been acknowledged in that paper. In addition the present authors wish to express their appreciation to Prof. Harlan Lewis and Mrs. Ruth P. Epling for assistance in collecting the later data, to Prof. G. Bartholomew and Mrs. Carolyn Mitchell for aid in preparation of the manuscript, and finally to Mr. J. C. Mitchell for preparation of the graphs.

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DISTRIBUTION OF FRESHWATER CHROOCOCCACEAE IN SZECHWAN, CHINA

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Introduction

The factors governing the distribution of freshwater algae are doubtless quite similar to those important to many other plants, differing only in magnitude, availability and specificity of effects. The persistence of an alga in any environmental complex simply attests to the fact that there is more or less favorable interaction between the hereditary mechanism of the plant and the influence of numerous internal and external factors. It is well known that some algae grow and multiply in certain habitats; others merely exist in such places; and some never appear there. Moreover, numerous species of algae are widely distributed in many habitats while others are confined to special and sometimes quite local areas. Some species occur regularly in the same waters year after year, and others appear only occasionally or rarely. Such diversity of response to environment among the many thousand species of algae makes difficult the drawing up of generalizations regarding algal distribution.

The Myxophyceae, or blue-green algae, completely lack sexual reproduction, and the hereditary mechanisms of these algae are practically unknown. They grow in habitats varying from aquatic to terrestrial, and from epiphytic to endophytic; they survive in ice and in hot springs having temperatures as high as 85° C; they occur in desert soil, tidal flats and many denuded soil areas; they flourish during the hot months of the year in shallow waters and often completely dominate the plankton of both fresh and salt water. These facts indicate that an explanation of the distribution of blue-green algae is not a simple one. It is important, however, that records be made of all data pertinent to their distribution.

G. S. West (1916) was among the first to attempt a grouping of fresh-water algae on an ecological basis. He established subaerial communities, associated species on dripping rocks, and aquatic communities, each with certain limiting subdivisions. On the basis of periods of greatest abundance, duration of vegetative cycles and times of sexual reproduction, Transeau (1916) divided the algae of Illinois into seven ecological groups: winter annuals, spring annuals, summer annuals, autumn annuals, perennials, ephemerals (mostly plankton), and irregulars. There is an abundance of literature dealing with the composition, permanence and kinds of algal aggregations, and Tiffany (1951) has summarized the more important of these contributions, listing six more or less distinct ecological communities: hydrophytes, edaphophytes, aerophytes, cryophytes, endophytes and epizoophytes.

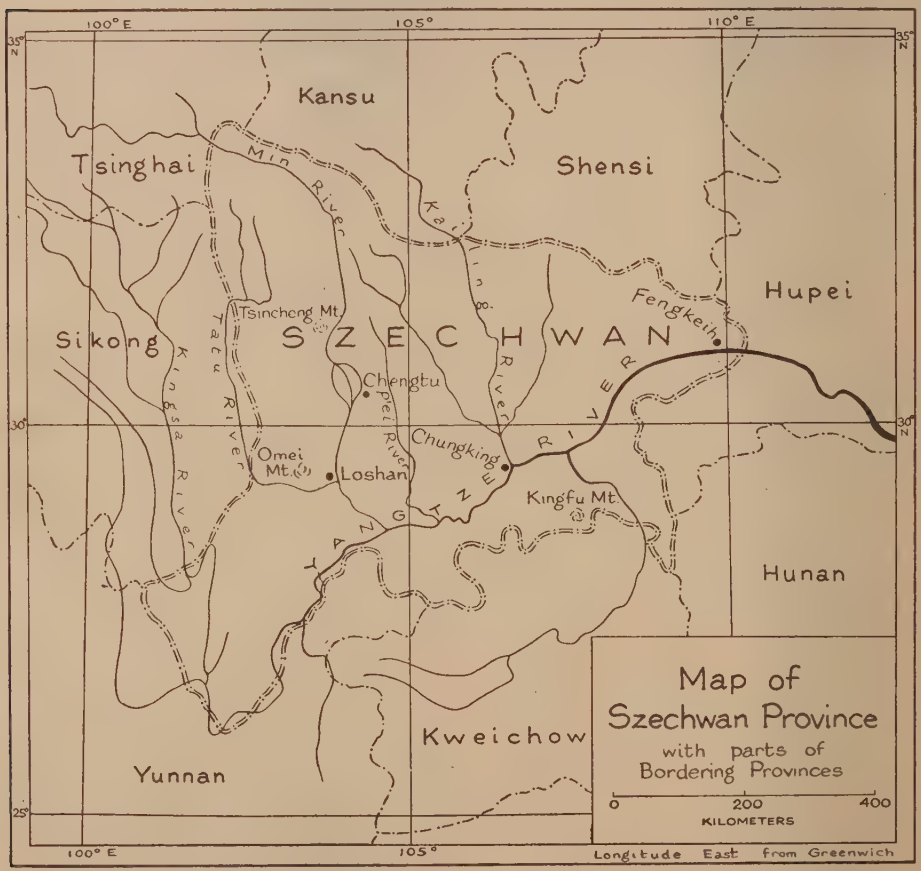
The Myxophyceae have received considerable attention in such ecological studies as indicated above. Special note has been made in many papers on the abundance and often preponderance of species of blue-green algae as epiphytes in moist tropical areas; as carpets on moist ground, damp stones and wet woodwork; as attachments to dripping rocks in ravines, and to stones and boulders over which water flows; as "water blooms" in lakes and ponds; and as living in

special habitats that may be calcareous, alpine, thermal, intertidal, endophytic or endozoophytic.

There are some eight families currently recognized as comprising the Myxophyceae (Drouet 1951): Chroococcaceae, Chamaesiphonaceae, Clastidiaceae, Stigonemataceae, Nostocaceae, Rivulariaceae, Scytonemataceae and Oscillatoriaceae. This paper deals largely with the distribution of the freshwater Chroococcaceae in Szechwan Province, China, although associated genera and species of other families are frequently mentioned to complete the picture. The Chroococcaceae are unicellular or more often colonial algae consisting of spherical, disclike or ovoid cells variously arranged in a conspicuous gelatinous envelope. Other blue-green algae may be filamentous, solitary or variously grouped into strata, cushions or spheres.

The Region Studied

The senior author collected some 6,500 specimens of blue-green algae from various parts of Szechwan from 1937 to 1946. The samples were taken from more than 500 stations widely distributed over an area of some 30,000 square miles. The area covered varied from gorge and lowland to mountain summit. Most of the collections were obtained periodically from January to March and from July to September, supplemented by a few samples secured during other months of the year.



The location of the principal stations may be noted from the accompanying map of Szechwan and parts of bordering provinces. The stations included:

1. Chungking and its environs: Yangtze valley, hills, mountains and rice fields.
2. Pe-P'ei and its suburbs, four miles north of Chungking: rapid streams and hot springs.
3. The Chungking-Chengtu Highway District, which is the central basin area of the Province.
4. Chengtu Plain (ricefield area of the Province): interconnected ditches and ponds covering an area of some 400 square miles.
5. Chengtu-Loshan Highway: narrow band of plains area on the banks of the Min River.
6. Loshan-Chungking area along the upper Yangtze River.
7. Chungking-Fengkeih Highway: mountainous area with rapid streams, dams and falls.
8. The areas occupied by the Tsincheng, Omei and Kingfu mountains.

Topographic and Climatic Features

Szechwan Province, located in mid-central China (see Map), has an area of 86,348 square miles. The Yangtze River has formed a precipitous gorge in a region a few miles wide near the eastern limits of the Province; elsewhere Szechwan is bounded by high mountains from branches of the Tsinling Range in the north and the Nanling Range in the south. The Yangtze River is the only natural means of communication by which Szechwan and other parts of China are connected.

The name "Szechwan" derives from the "Four Rivers" which are the principal tributaries of the Yangtze in the Province, flowing from the north: Tatu River, Min River, P'ei River and Kialing River, named from west to east. Two tributaries from Kweichow and Yunnan provinces flow into the main artery from the south and southwest. The Yangtze itself has two main sources rising in the snowy heights of Tsinhai and Sikong provinces north and west (see Map).

Largely as a result of its geographic location and topographic features Szechwan has a temperate and moist climate. Due to the high mountains the moist winds from the Pacific lose much of their moisture, and the cold dusty Siberian winds are restricted in their intensity. Despite its location in the interior of a continent, Szechwan is protected from extremes of temperature by the surrounding mountains, and the contrast between summer and winter is not great. Summer temperatures seldom exceed 38° C and winter temperatures rarely drop below freezing in the central basin of the Province. Severe frost is uncommon in the basin. In the higher elevations, such as the mountains of Omei, Tsincheng and Kingfu, the temperatures are lower and snow is normal after September.

Humidity is high, and clouds and mists are common in winter months. In Chungking in the south the sun can seldom be seen from December to February. During the "mold period" of summer months the humidity is very high. Moisture condenses on all cool objects, and walls and ceilings drip with water. Mists, covering the whole region for long periods during the year, lessen the evaporation of water and thus contribute toward the often luxurious growth of subaerial and soil algae, as well as other plants.

Total precipitation in winter is very light, although it may rain for a few days at a time. The period of greatest rainfall begins in May and reaches a maximum in June and July, sometimes extending into August.[1] In some localities there may be another increase in September, decreasing again in November. The mean annual rainfall varies from 75 mm. to 200 mm. a month. During the months of May, June and October occasional heavy

[1] See Chu and Cooper (1950) for additional climatic data on the region around Chungking.

rains may result in such rapid rises of water in the rivers as to cause overflow and washing away of the soils of the lower fields. Thus lower areas may be completely flooded by such sudden rises, and this undoubtedly is favorable to the dissemination of the algae. Upon lowering of the water level, particularly in winter, the attached algae become exposed on rocks and stones, but desiccation is limited by the cloudy and humid atmosphere.

Ecological Habitats and Their Algal Constituents

In spite of some overlapping the major ecological habitats in which regular collections were made over a ten-year period may be separated into (1) subaerial, (2) edaphic, (3) aquatic, and (4) special environments. In Table I is given a summary of the genera and species occurring in each of the first three habitats listed. Data on special environments are meager and will be discussed later in the paper. The tabular summary includes the species found regularly year after year at the various collecting stations. The rarely occurring algae have been omitted because of uncertainty regarding their significance in the communities. Sufficient material was not always available to make identification of some of these algae certain.

Table I. *Habitat distribution of Chroococcaceae of Szechwan, China*

Genus and species* of Chroococcaceae	Edaphic and subaerial						Aquatic					
	Floor of pine forest	Tree bark, walls of buildings	Sandy rocks	Walls of mountain caves	Dripping rocks, cliffs, dams	Wet rocks at spring outlets	Puddles and rain pools	Ponds and reservoirs	Rapid streams and brooks	Cold springs and wells	Hot springs	Salt marshes, brackish water
Aphanocapsa												
biformis A. Braun		x		x				x				
delicatissima W. & G. West								x				
elachista W. & G. West					x		x	x	x	x		
grevillei (Hass.) Raben.	x	x	x		x	x			x			
montana Cramer	x			x	x							
pulchra (Ktz.) Raben.								x				
thermalis Bruegg.											x	
Aphanothece												
castagnei (Breb.) Raben.	x			x	x							
microscopica Naeg.				x	x							
naegelii Wartm.		x		x	x				x			
nidulans P. Richt.	x		x	x	x							
pallida (Ktz.) Raben.	x	x	x	x	x	x			x			
stagnina (Spreng.) A. Braun				x				x		x		
Chroococcus												
cohaerens (Breb.) Naeg.	x				x							
dispersus (Kies.) Lemm.				x	x		x					
giganteus W. West								x				
helveticus Naeg.		x	x	x	x	x						
lithophilus Erceg.				x								
minor (Ktz.) Naeg.	x	x	x	x	x	x		x	x	x	x	
minutus (Ktz.) Naeg.	x	x	x	x	x	x		x	x	x	x	x
schizodermaticus W. West			x	x				x				
tenax (Kirch.) Hier.		x		x	x	x						
turgidus (Ktz.) Naeg.	x	x		x	x	x			x	x	x	x
turicensis (Naeg.) Hansg.				x	x	x			x			
westii (W. West) Boye-Peters.				x	x				x	x		
Coelosphaerium												
kuetzingianum Naeg.								x		x		
minutissimum Lemm.												x
Dactylococcopsis												
rhaphidioides Hansg.	x							x		x		

TABLE I—*Continued*

Genus and species* of Chroococcaceae	Edaphic and subaerial						Aquatic					
	Floor of pine forest	Tree bark, walls of buildings	Sandy rocks	Walls of mountain caves	Dripping rocks, cliffs, dams	Wet rocks at spring outlets	Puddles and rain pools	Ponds and reservoirs	Rapid streams and brooks	Cold springs and wells	Hot springs	Salt marshes, brackish water
Gloeocapsa												
alpina Naeg.			x	x	x	x				x		
atrata (Turp.) Ktz.			x	x	x				x			
calcarea Tild.			x	x	x							
compacta Ktz.	x	x	x	x						x		
crepidium Thur.												x
gelatinosa Ktz.				x	x						x	
gigas W. & G. West					x	x						
kuetzingiana Naeg.		x	x	x	x	x						
magma (Breb.) Hollerb.			x	x	x	x						
montana Ktz.	x				x							
ralfsiana (Harv.) Ktz.		x		x	x	x						
rupestris Ktz.		x			x				x			
sanguinea (Ag.) Ktz.				x	x							
thermalis Lemm.											x	
Gloeothece												
confluens Naeg.		x	x		x							
dubia (Wartm.) Geitl.					x							
fusco-lutea Naeg.	x	x			x		x					
rupestris (Lyng.) Born.		x			x	x				x	x	
samoensis Wille		x			x							
Gomphosphaeria												
aponina Ktz.							x					
Merismopedia												
convoluta Breb.							x			x		
glauca (Ehr.) Naeg.						x	x		x	x		
Microcystis												
aeruginosa Ktz.					x			x	x			
incerta Lemm.	x	x	x	x		x	x	x				
Synechococcus												
aeruginosus Naeg.		x						x				
elongatus Naeg.	x				x							
Synechocystis												
aquatilis Sauv.					x		x	x			x	
Total no. of genera	8	7	6	5	9	7	7	6	6	7	6	4
Total no. of species	14	19	15	28	38	16	8	14	14	12	10	5

* For the sake of consistency we have used the nomenclature of Geitler (1932). Drouet (1943) and Drouet and Daily (1948) have suggested certain nomenclatural transfers and synonymy in the Chroococcaceae, but until their investigations cover the group as a whole, it seems best here to use the more familiar epithets.

Subaerial communities of aerophytes

The separate subaerial habitats fall naturally into two divisions, depending primarily upon the constancy of the water supply. The more nearly aquatic dripping rocks of cliffs, dams and falls, and the outlets of springs and rivulets on slopes are quite distinct most of the year from the drier subaerial situations, such as bark of trees, damp walls of buildings, woodwork; sandy rocks, granite rocks and limestone cliffs; and walls of caves.

Bark of trees, damp walls of buildings, piles, wharves, and other such exposed places.—These exposed surfaces are more or less moist throughout the year and are often covered with green and blue-green strata, especially on the north and more shaded sides. Blue-green algae, both colonial and filamentous, are associated

with green algae, mosses and often small ferns. The Chroococcaceae, often dominated by *Gloeothece fusco-lutea* and *Chroococcus minutus,* consist of 7 genera and 19 species (Table I).

Sandy rocks, granite rocks and limestone cliffs.—These situations, in contrast to those just discussed, are generally more arid, exposed to sun and wind. They are washed by water in the rainy seasons, but remain damp for only a few hours at a time. Little vegetation is found here except for blue-green algae, which form small to large sheets over the surfaces, blackish when dry and olive-green after rains. Deeply colored gelatinous sheaths envelope the cells, and the contents of the protoplasts may be black, brown, red or yellow. The Chroococcaceae, growing intermixed with elements of Scytonemataceae, Stigonemataceae and Nostocaceae, are represented by 6 genera and 15 species. It will be noted from Table I that 9 of these species also occur in the more moist subaerial habitats.

Walls of deep caves in the mountains.—These areas are similar to the rocks and cliffs just described, but are more protected from wind and sun. They extend up the mountains some 2,000 meters. The Chroococcaceae found growing here are highly colored, gelatinous forms associated with members of Scytonemataceae, Stigonemataceae, Nostocaceae and Rivulariaceae. The algae grow abundantly on the rocky walls at the entrances to the caves. The number of individuals as well as species gradually decreases toward the recesses of the caves until light is insufficient for their growth. The Chroococcaceae identified consisted of 5 genera and 28 species, of which 13 species are also common in the drier rocky areas (Table I). The blue-greens growing sparingly in the deepest recesses of the cave number only 2 genera and 7 species, but they all also occur in the more intensely illuminated entrances to the caves.

Dripping rocks, cliffs, dams and falls.—The Chroococcaceae found on the nearly vertical surfaces of such constantly moistened areas are always mixed with diatoms and desmids and form large patches of olive-green or light blue-green masses. Sometimes filamentous blue-green algae or *Chantransia* stages of red Florideae are important constituents of the algal group. The blue-green patches of algae may reach altitudes of some 2,000 meters. This is the most persistent of all the subaerial communities and is made up consistently of the largest number of species. There are 38 species of Chroococcaceae distributed among 9 genera (Table I). Twenty-three of these species are also found at the entrances to the rocky caves.

Wet rocks at the outlets of springs and rivulets.—The ecological situation here is quite different from any so far discussed. The surface of the rock is constantly washed by cold water that remains at a temperature of about 10° C throughout most of the year, except during the winter, and may be flooded for short periods of time during the melting of the snow in spring and in the rainy season of early autumn. The Chroococcaceae are always associated with filamentous blue-greens, mosses and liverworts, and form olive-green, brownish green or yellowish red strata on the rocks or even on tree roots extending into the springs. Although 7 genera and 16 species are listed in Table I, the dominant plants belong to the genera *Aphanocapsa, Chroococcus, Gloeocapsa* and *Gloeothece.*

Forest floor of edaphophytes

On the floor of the pine forests with their moist soils and diffuse light occur good growths of Chroococcaceae from March to November in the Red Basin region and from April to October in the higher mountainous areas of Omei, Kingfu and Tsincheng. Terrestrial species of *Ulothrix* and *Zygogonium* (Chlorophyceae), as well as other green algae, are always associated with the blue-greens. The dominant Chroococcaceae are *Aphanocapsa grevillei, Aphanothece nidulans,*

A. pallida, Chroococcus minutus, C. turgidus, Gloeocapsa montana and Gloeothece fusco-lutea, among the 8 genera and 14 species listed in Table I.

Aquatic communities: hydrophytes

The aquatic environments in mountainous Szechwan differ considerably and will be discussed here under six habitat categories, three of which are quite specialized: (1) puddles and rain pools, (2) ponds and reservoirs, (3) rapid streams and brooks, (4) cold springs and wells, (5) hot springs and (6) salt marshes and brackish waters. The diversity of species from habitat to habitat is more evident than in the subaerial communities.

Puddles and rain pools.—These temporary bodies of water support an algal flora of few species, often almost a natural culture of one species. The chief Chroococcaceae are *Aphanocapsa elachista, Chroococcus dispersus* and *C. limneticus,* associated rarely with species of *Gloeothece, Microcystis, Merismopedia,* and *Synechocystis*; and with unicellular Chlorophyceae (*Chlorella, Chlamydomonas*) and Euglenophyceae (*Phacus, Trachelomonas*).

When stream flow recedes in the winter, rocky pools appear in the stream bed, containing species of *Aphanothece, Chroococcus, Microcystis* and *Merismopedia,* along with depauperate specimens of filamentous greens and blue-greens.

Ponds and reservoirs.—Natural ponds are not common in Szechwan except in the Chengtu Plain. Artificial ponds may be found occasionally in school gardens or on the grounds of the wealthier landowners. Reservoirs, dug for irrigation and to supply drinking water, are rare. These bodies of water are generally fairly permanent from year to year. From March to May and during September and October they are covered with extensive water blooms, dominated by *Microcystis flos-aquae, M. aeruginosa* and *Coelosphaerium kuetzingianum.* Ten additional species representing 4 genera are also present but never reach water-bloom proportions (Table I).

Rapid streams, brooks and rivulets.—These rapidly moving waters are well aerated and contain a small number of Chroococcaceae, largely epiphytic and distributed among 6 genera. The larger filamentous algae are the red *Lemanea* and *Thorea,* the green *Cladophora* and the blue-green *Plectonema, Tolypothrix* and *Nostoc.*

Cold-water springs and wells.—These waters maintain a rather uniformly cold temperature throughout the year (10–12° C), are generally very clear and highly charged with bound carbonates. Often the red *Batrachospermum* is the typical inhabitant, together with less abundant species of *Spirogyra* and *Vaucheria.* The Chroococcaceae may grow in such habitats as free-floating plants, form mucous strata on submerged stones, become attached to roots and stems of higher plants, or grow intermingled with other algae. They are made up of some 7 genera and 12 species. *Eucapsis alpina* Clements and Shantz is a rare constituent of the cold-water springs.

Hot springs.—The dozen or more hot springs visited in Szechwan have temperatures varying from 50° C to 75° C, occasionally up to 80° C. The chief algae able to survive in such temperatures are the filamentous blue-green *Oscillatoria, Lyngbya, Phormidium* and *Symploca,* with diatoms and a few desmids. The associated Chroococcaceae, not nearly as abundant as the other algae, comprise 6 genera and 10 species (Table I).

Salt marshes and brackish waters.—The Tzu-Lin-Tsing district of Szechwan is a salt-manufacturing center, and the several outlets, ponds and ditches are quite saline, although the degree of salinity varies considerably because of the rains. Only *Chroococcus turgidus, C. minutus, Gomphosphaeria aponina, Gloeocapsa crepidium* and *Coelosphaerium minutissimum* were collected in such habitats during the ten-year period of study, and

they were never abundant. Species of filamentous blue-green *Lyngbya, Oscillatoria, Microcoleus* and *Spirulina* have also been collected.

Algae of special habitats

Certain Chroococcaceae were found embedded in Paris-green colored crusts of calcium carbonate, often near springs, wells or dripping rocks. These were *Gloeocapsa incrustata, G. calcarea,* and *Gloeothece confluens,* usually associated with filamentous blue-greens, such as *Scytonema, Petalonema, Rivularia* and *Schizothrix. Aphanocapsa anodontae* Hansg. was frequently found on shells of Mollusca. *Aphanothece lemnae* Chu was isolated from the intercellular spaces of a duckweed (*Lemna* sp.).

The water of roadside ditches near cities and villages is usually nearly quiescent, poorly aerated, often stagnant, and supports a large bacterial population. The algae found in such ditches are largely members of the Euglenophyceae, Chlamydomonadaceae and the Oscillatoriaceae. They are never abundant. The Chroococcaceae are rare and only two species were collected: *Chroococcus turgidus* and *Merismopedia tenuissima* Lemm. Ditches situated near foothills have constantly flowing water, and their algal flora is similar to that of brooks and rivulets discussed earlier.

The interconnected rice fields, often terraced from base to mountain summits up to 2,000 meters, have an algal flora quite similar to that of ponds and reservoirs, except that water blooms do not occur. This lack of great masses of plankton is probably due to the constant "flow" of water from one level of rice fields to a lower one.

Discussion and Summary

Drouet (1950) is convinced from his study of thousands of unicellular blue-green algae from all parts of the world, particularly herbarium specimens, that the species of Chroococcaceae are actually few in number (perhaps two dozen) and widely distributed. Insufficient ecological data are at hand to make any statements regarding "growth forms" of these algae or even very clearly to evaluate naturally occurring species and varieties. There is no possibility of exploring the situation from the standpoint of establishing such categories as cenospecies, ecospecies or ecotypes proposed by Turesson (Clausen, Keck and Hiesey 1940) for vascular plants, because of the lack of any known method of genic exchange in the blue-greens. Cultural studies have not progressed far enough to indicate the extent of morphological variation under different controlled environments, although such reports as those of Pringsheim (1950) and of Gerloff, Fitzgerald and Skoog (1950) indicate a fertile field for further investigations.

It is undoubtedly true that the value of some generic delimitations is very difficult to assess in the Chroococcaceae, to say nothing of the differences among the species and varieties that have been described. Numerous species have, however, been described from time to time, and phycologists have inadvertently or not been able to identify many of them on the basis of what appear to be diagnostic characteristics. In most instances the mass appearance of the plants has probably not been a major consideration, and the size, color, protoplasmic contents and variations in sheaths of cells may have been given too much weight. If it could be established that there are certain "species complexes" that include some of our currently recognized species, the blue-greens would represent a group of organisms almost ideal for ecological study. The investigator would not have to be on the look-out for genetic variations caused by polyploidy, introgressions, linkage, crossingover and other ills resulting from hybridization. At present our only recourse appears to lie in accepting such species of Chroococcaceae as seem to be valid and proceeding

on that basis until more data are available. It is from this viewpoint that the authors have attempted to analyze the ecological significance of this ten-year assembly of data on the Chroococcaceae of Szechwan.

A glance at Table I indicates that 55 species of Chroococcaceae have been identified from all habitats: 42 species occur in the subaerial communities, 34 in the strictly aquatic habitats, 14 in the sole edaphic situation studied, and a much lesser number of species in each of the special habitats. This suggests, as would be expected, that extremes of temperature, lack of light, salinity or other factors may seriously limit the growth of freshwater Chroococcaceae; and that these plants grow well in a considerable range of ecological niches where such extremes do not obtain.

In the subaerial situations the largest number of species occurs where the water supply is most continuous; the least number on sandy rocks and the outlets of cold springs. The number of species in the aquatic habitats is largest in the ponds and streams, and least in hot springs and saline waters. Fourteen species were found on the floor of the pine forests.

If we consider 8 of the ecological niches listed in Table I and omit the cold and hot springs and the saline waters as more specialized habitats, it is evident that—

0 species and 3 genera occur in all habitats
2 species and 1 genus occur in 7 habitats
2 species and 1 genus occur in 6 habitats
2 species and 1 genus occur in 5 habitats
8 species and 1 genus occur in 4 habtitats
14 species and 1 genus occur in 3 habitats
10 species and 2 genera occur in 2 habitats
9 species and 1 genus occur in 1 habitat.

Stated differently, the genera *Aphanocapsa, Chroococcus* and *Microcystis* are represented by one or more species in all habitats; *Aphanothece* in 7; *Gloeocapsa* in 6; *Gloeothece* in 5; and the remainder of the genera in 4 or fewer habitats. This indicates that distributional data on the basis of genera alone tell an incomplete story, since several species may be involved, each with its own distribution which may or may not coincide with that of other species of the genus. The data also seem to show that few of the species —if their identification can be relied upon —are widely distributed in Szechwan, and that there is a relationship between a given species and the ecological niche in which it grows and grows best.

The authors express their indebtedness to Miss Jane W. Roller for the final draft of the Map of Szechwan; to Professor Francis L. K. Hsu of Northwestern University for aid in checking certain place names; and to Professor M. E. Britton of Northwestern University for helpful suggestions during the preparation of the manuscript.

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CHANGES IN THE YELLOW PERCH POPULATION OF LAKE MENDOTA, WISCONSIN, BETWEEN 1916 AND 1948[1]

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INTRODUCTION

Many investigations of marine fish populations have been made during the last few decades. These were often prompted by a serious reduction in commercial yields and there usually followed in their wake restrictions on fishing and other conservation measures. In smaller inland lakes of this continent commercial fishing is relatively rare, and angling solely for recreation represents man's most important direct influence on the fishes present. There are few such lakes where the available information permits us to follow the fate of one particular species of fish over more than a human generation.

One of the few is Lake Mendota, Wisconsin, and this report is an attempt to trace the changes in its population of yellow perch (*Perca flavescens* Mitchill) during the last 50 years. For the following reasons this lake is particularly well suited for such a study: (1). It was much influenced by human development because the rapidly growing city of Madison partly surrounds it. (2). Its limnology has been more intensively studied than that of any other lake in the world. (3). Yellow perch are by far the most abundant panfish in the lake. (4). Commercial fishing as such was never legalized there although large numbers of perch were removed from the lake in early settlement days.

The two main changes among the perch in Lake Mendota, to be discussed later in more detail, were a decrease in the number of fish and an increase in their size. Such a gain in size has often been observed as the result of a reduction in the number of fish present (Alm 1946; Eschmeyer 1937, 1938; Hile 1936; to mention only a few examples of fresh water studies). If the fish were stunted before removal began, the effect of reduction in number usually appeared as a very rapid increase in size. There is, however, one recent example where such a reduction among the adult fish had no appreciable effect on their size. The perch (*Perca fluviatilis* L.) of Lake Windermere, England, recently reduced to about 1/15 of their previous numbers, did not show any significant gain in size (LeCren 1949). This fish population is still under observation and it is well possible that the effects of the removal will eventually be reflected in the growth rate.

In the case of the Mendota perch there is also sufficient information available[3] to discuss some of the causes for the observed changes. Among those are: competition with other fish, epizootics, and fishing pressure. There is little, if any,

[1] These studies were supported jointly by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation, and by the Wisconsin Conservation Department. The author also wishes to express his thanks for much help he received in the collection of material for this study and for advice from E. D. LeCren, J. C. Neess, and W. E. Ricker; to the Lake Laboratory personnel of the University of Wisconsin, especially Mr. J. Budd; furthermore to the Wisconsin Conservation Department for access to their scale collections and files and to A. D. Hasler for advice and encouragement in the course of the investigation and for making available manuscripts from student projects in addition to data assembled by laboratory personnel.

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[3] The bulk of the material referring to the years 1946 to 1949 was taken from the author's doctoral dissertation submitted to the Department of Zoology at the University of Wisconsin, entitled "Contribution to the ecology of the yellow perch (*Perca flavescens* Mitchill) in Lake Mendota, Wisconsin."

direct evidence that would permit the assessment of one more important factor, namely the changes in the food supply of the fish.

Decrease in the Number of Perch

There is considerable evidence for a falling off in the numbers of perch between the early nineteen hundreds and the present. This is derived from the following sources: (1) catches of perch in experimental gill nets; (2) newspaper and historical reports of angling successes and recent creel censuses; (3) population estimates.

Gill netting. Records of perch taken in gill nets have been kept by the Zoology Department of the University of Wisconsin since 1942. Recent average numbers in the catches can thus be compared with those before 1920 (Pearse and Achtenberg 1920) and used to illustrate the relative abundance of the fish at these two stages of the century (Tables I and II, Fig. 1).

Catches made during the spawning season in the spring and other net hauls made in August indicate that the perch in 1916 were considerably more numerous than in 1947. The catch per unit of effort was 4.3 times as great in the spring and 2.4 times as great in the summer, or 3.3 times on the average. It should be added that the mesh size used in 1947 was larger than that employed in 1916. The perch, however, as will be shown later, were larger as well.

While gill nets are selective as to the sizes of fish they can catch, there is a range of fish size rather than an absolute size corresponding to each size of mesh. Thus it appears likely that the smaller nets in 1916 and the somewhat larger ones in 1947 both caught equally representative samples of the mature (spawning) population. These data might therefore well serve for the comparison.

Newspaper reports and creel census information. An illustration comparing conditions in 1900 and 1916 can be quoted

Table I. *Comparison of gill net catches of yellow perch in Lake Mendota, Wis. during the spawning seasons of 1916* and 1947†, from nets set close to shore at 4–10 m. depth‡*

1916					1947				
Date	No. of perch caught	Length of net (feet)	Hrs. in water	Foot-hours of net-set	Date	No. of perch caught	Length of net (feet)	Hrs. in water	Foot-hours of net-set
April 21	6	60	14	840	April 20	32	50	20	1,000
April 28	163	75	14	1,050	April 21	149	300	19	5,700
April 28	380	75	14	1,050	April 22	60	25	22	550
April 30	8	60	3	180	April 24	36	25	18	450
April 30	11	60	4	240	May 10	39	50	23	1,150
May 2	17	60	5	300					
May 2	23	60	3	180					
May 2	18	60	3	180					
May 6	8	60	1	60					
Totals	634			4,080		316			8,850
Perch caught per 100 feet of net per hour:	15.5					3.6			

* From Pearse and Achtenberg (1920).
† From records of the Lake Laboratory, University of Wisconsin.
‡ Out of the many net records, only those given here are comparable in being set at similar times of day, in similar locations and during comparable seasons. Nets used in 1916 were 1 inch bar mesh, those in 1947, 1¼ inches bar mesh.

TABLE II. *Comparison of gill net catches of yellow perch in Lake Mendota, Wis., during the summers 1916 and 1947, from nets set at 6–9 m. depth. See footnotes to Table I*

1916					1947				
Date	No. of perch caught	Length of net (feet)	Hrs. in water	Foot-hours of net-set	Date	No. of perch caught	Length of net (feet)	Hrs. in water	Foot-hours of net-set
Aug. 10	118	60	5	300	Aug. 4	1	25	4	100
Aug. 12	71	60	4	240	Aug. 5	7	25	4	100
Aug. 13	72	60	4	240	Aug. 5	3	25	4	100
					Aug. 5	19	25	4	100
					Aug. 6	1	25	4	100
					Aug. 6	54	25	4	100
Totals	261			780		85			600
Perch caught per 100 feet of net per hour:	33.5					14.2			

from Pearse and Achtenberg (1920): "The old fishermen claim that many more fish were caught 15 years ago and state that a single man *sometimes* [authors' italics] secured over 800 perch a day. At present (1916) the usual catch of a professional fisherman, fishing through the ice with a line and two hooks, is from 200 to 400 perch per day."

This can be contrasted with creel census figures, obtained independently by the Wisconsin Conservation Department and University Survey crews. An average daily catch of 10 perch per man-day of angling through the ice was given by both sources with hardly any fluctuations during the winters of 1947, '48 and '49 (Mackenthun and Herman 1949).

Population estimates. It is mentioned by Pearse and Achtenberg (1920) that Lake Mendota could have supported a population of ca. 15,000,000 adult perch in 1916. This rough estimate was based on the amount of perch food which these investigators assessed to be present in the lake and the observed rate of feeding among the perch which they kept in aquaria. From gill nettings at the spawning sites and from the recapture of tagged fish a more recent figure can be computed. Between 2,000,000 and 4,000,000 adult perch were estimated to inhabit Lake Mendota during the summer of 1949; the latter figure as well as the estimate from 1916 represent maxima and are therefore considered comparable. The estimate based on tagging is, however, subject to the customary difficulties and errors connected with the tagging method of population assessment and both population estimates are cited here merely as supporting evidence for the decline in numbers of fish since 1916.

It is interesting that the population estimates for 1916 and 1949 illustrate a decrease in numbers comparable indeed to that which was shown by gill netting, namely, a reduction to about ⅓ or ¼ of the 1916 level. A comparison of early and recent creel census figures would tend to indicate a greater decline. It is believed that the early estimates of daily catches really were maxima and that they should not be taken as a basis for numerical computations.

One may finally note the introduction of a daily legal limit of 30 perch in 1927 (now reduced to 25), and, a few years later, the establishment of a closed season. It is open to question whether the introduction of such measures reflected the trend towards fish conservation in general or a particular need for it in Lake Mendota; the author is inclined to the former interpretation.

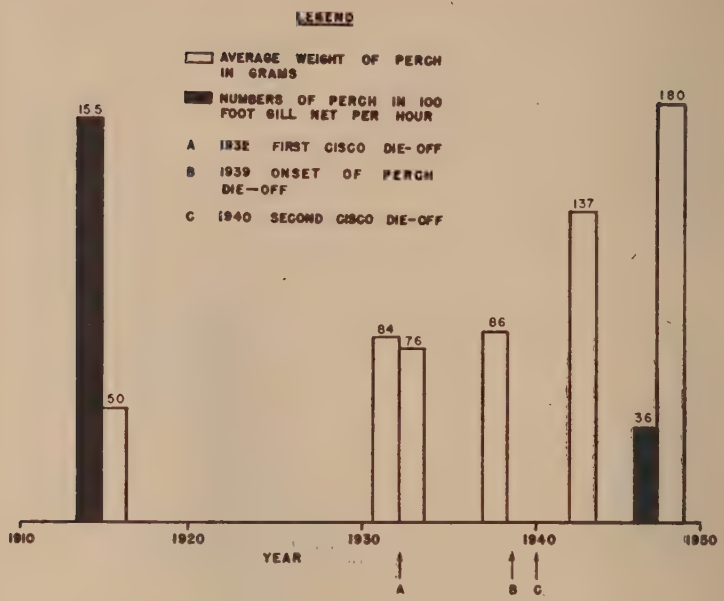

FIG. 1. Comparison of average weight and numbers of yellow perch (*Perca flavescens* Mitchill) from gill netting records in Lake Mendota, Wis., between 1916 and 1948.

INCREASE IN AVERAGE SIZE AND GROWTH RATE

The earliest reliable measurements date from 1915 and 1916. The perch these refer to could, unfortunately, not be assigned to their proper age groups since no scales were taken from them. They were, however, described as "mature fish" (Pearse and Achtenberg 1920). Apparently they were from the middle part of the spawning size range of the time and hence presumably between three (3) and seven (7) years old. Their size and weight is compared with the respective averages in samples of adult perch which were taken in different years after 1916 (Table III, Fig. 1).

In 1931 some of the fish were captured by seine, a non-selective gear with respect to fish size. The remainder of the sample from 1931 and all subsequent samples were taken by gill nets of several mesh sizes so as to assure a minimum of selectivity. The nature of the sample from 1916 has already been discussed.

It is interesting that the average weight increased from 50 to 180 grams, or 3.6 times; almost the same as the decrease in abundance (3.3) estimated earlier. There are no data to indicate whether the increase in size and weight between 1916 and 1931 was steady or discontinuous. The samples from 1932 and 1939 are the smallest we have and the discontinuity of increase in size and weight which they illustrate may well be due to sample size rather than to true fluctuations; they are included in the table with this caution.

An examination of the figures from the remaining years makes it permissible to assume that the increase in growth rate was not a steady one. In a period of twelve years, between 1931 and 1943 sizes (total length) and weights of the perch in Lake Mendota increased by 16 mm. and 42 grams, respectively. Contrasted to this there may be noted the larger gain of 29 mm. and 52 grams between 1943 and 1948, in a period of five years only.

TABLE III. *Average total length and weight of adult yellow perch in Lake Mendota, Wis., between 1916 and 1948*

Year of capture..	1916	1931	1932	1939	1943	1946	1948
Number of fish in sample	169	261	51	25	297	375	210
Average total length in mm.	162	198	180	188	214	220	243
Average weight in grams	50	84	76	86	128	137	180

Even if one were to rely on the figures of the small sample from 1939, it will be apparent that the most substantial acceleration in growth rate happened unquestionably in the last quarter of the 32 years of observation. In the same period there occurred a severe disease among the perch, a reduction in numbers among a competing species and, possibly, some increase in fishing pressure. Previous brief references to this size increase have been made by Hasler (1945) and Mackenthun and Herman (1949).

Discussion of Environmental Influences

Diseases and parasites. The first indication of fish epizootics in Lake Mendota was a mass die-off of fish in 1884, one of the earliest incidents of such nature in a large inland lake of this continent to have been investigated by the biologists of the day (Forbes 1890, Dunning 1884). Over 200 tons of dead fish, mostly perch, were hauled away by Madison city disposal crews. No external or internal parasites could be detected; suggestions were made, though without evidence, that food organisms from deeper regions of the lake had caused the sudden die-off.

Today the perch in Lake Mendota are hosts to a micro-organism which affects them seriously. Yet it should be added that the perch in this lake are, at the same time, relatively free from most other common fish parasites (Bangham 1947). This infectious perch disease was noted when its first serious outbreak occurred in the summer of 1939, though it was probably present earlier. The disease with its red sores and open lesions is caused by a myxosporidian of the genus *Myxobolus*. Many thousands of perch died from it every summer between 1940 and 1946 and the most serious yearly outbreaks coincided with the onset of hot weather in mid-July. Since 1946 the epizootics abated and far fewer perch seemed affected during 1948 and 1949.

Perch caught in gill nets between 1946 and 1948 were examined for the incidence of infection among the various size- and age-groups. It was found that the percentage of infection was much greater among older fish in the samples (Table IV). This apparent selectivity of the disease for older fish may only illustrate that the chances of infection become greater the longer the host is exposed to invasion by the parasite. It need not be assumed that the younger fish are more resistant to the micro-organisms.

Competition and predation. Birge (1922) referred to the large-scale die-off among the perch and other fish, reported from 1884, when he commented on the increasingly larger perch to be found in Lake Mendota. He suggested that the remaining population experienced great relief from intraspecific competition and perhaps also from predation during early life by the removal of large numbers of older perch. Comparable ideas were expressed by Ricker and Foerster (1941, 1948) in discussions of the respective sizes of sockeye salmon yearlings in Cultus

TABLE IV. *Incidence of sporozoan infection among the yellow perch of Lake Mendota, Wis., caught in the winter 1946/47*

Age in years	Total number of perch caught	Number of healthy perch	Number of diseased perch	Percentage of infection
2	7	7	0	0
3	44	42	2	4.5
4	177	137	40	22.6
5	46	22	24	52.0
6	3	1	2	66.6
Totals	277	209	68	24.6

Lake, British Columbia. In Lake Mendota it is not only the perch, however, which have undergone an appreciable drop in numbers during the present half-century. Another fish, the cisco (*Leucichthys artedi* LeSueur), once extremely plentiful, has been reduced very severely during that period. The case of the cisco should be given a brief review here since it appears to be closely related to that of the perch.

In 1932 and again in 1940 large numbers of dead cisco suddenly appeared floating on the surface during the hot summer months; here again, as in 1884, no internal or external parasites were apparent and biologists had to look elsewhere in order to explain this sudden die-off.

In most lakes the cisco is narrowly limited to its oxygen requirements and less well adapted to stand high temperatures than most warm water species. Some varieties, however, inhabit shallow eutrophic lakes as far south as Indiana.

It has as yet not been explained what caused this severe reduction among the cisco. Climatic conditions may have affected the thickness of the metalimnion in certain years. Thus there might have been, at times, a very narrow zone where optimum temperature conditions coincided with an adequate supply of dissolved oxygen for this delicate fish.

Furthermore, heavy summer blooms of blue-green algae are a sporadic occurrence on Lake Mendota. A depletion of dissolved oxygen in the metalimnion could well be accentuated by local concentrations of decomposing phytoplankton. The author found that accumulations of phytoplankton below the surface can reach considerable density. After a bloom of *Gleotrichia* during late June of 1948 a suspension of these algae was so thick at the 6 m. level (the upper boundary of the thermocline) that tow-samplers could hardly be operated. Moore (1950) described comparable local plankton concentrations in some Louisiana lakes where they appeared to coincide with a die-off among the more delicate fish.

Suspension gill nets of different mesh sizes have been set in the thermocline region during the summer months of 1949. These caught perch and cisco only and illustrated that the two fish occupy the same region, at least during a part of the summer.[4] Thus it seems that there could well be some competition for space between the perch and the cisco.

While the cisco feed predominantly on zooplankton (Langford 1938), the diet of the perch is more varied. Pearse and Achtenberg (1920) and Langford and Martin (1940) have shown that perch draw on bottom organisms and plankton for their diet, depending on the seasonal availability or preponderance of either. Perch stomachs, taken during the evening movements of these fish towards the shore in the summer months, frequently contained nothing but pelagic zooplankters (Hasler and Bardach 1949). Thus a glance at the food habits of both species further indicates that some competition might have existed for food as well as for space. It is impossible to estimate in retrospect the extent to which the decline in the cisco population has contributed to the changes in perch growth. It must suffice here to point out the possibility of competition and to stress the coincidence in time between the rapid gain in perch sizes and the decline in the number of cisco in the lake.

No study of predation on the perch in Lake Mendota has been made; even the occurrence of cannibalism, mentioned earlier, is based on circumstantial evidence. From field observations it appeared that the northern pike (*Esox lucius*) was the most serious perch predator, feeding on fry, juvenile and also adult perch. Various centrarchid fishes, the long-nose gar (*Lepisosteus osseus*) and the dogfish (*Amia calva*) were next in importance. Mammals and birds were found of little or no consequence as perch predators, especially if the removal of perch by man is not considered as predation.

[4] Antonie, J. E. 1949, "Locating the cisco," an unpublished manuscript on file at the Zoology Department, University of Wisconsin.

Fishing pressure. Recent counts of anglers during the ice fishing season showed that the perch of Lake Mendota yearly attract several thousand fishing enthusiasts from near and far. A comparable number of anglers can also be found on the lake during the summer months.

The decline in the number of perch in the lake occurred during a period in which the population of Madison increased considerably and road travelling became easier and more comfortable. Even though reliable counts of anglers have only been made since 1946, it is likely that the ice-fishermen on Lake Mendota were fewer in numbers before 1920 than after 1940. Provided they spent a comparable amount of angling time, it may be said that fishing pressure has increased during that period. The angling success has decreased when one compares the numbers of fish caught then and now, but the increased size and weight of the fish tend to make up for the reduction in numbers.

In this connection it is suggestive to examine some figures given elsewhere in this article. The daily winter creel in 1947, '48 and '49 was around 10 perch per man-day; a total of 60,000 to 100,000 perch were removed by the 6,000 to 10,000 anglers reported on the lake during any one of the three winters referred to above (Mackenthun and Herman 1949). The catches of earlier years, namely 200 perch per day in 1916, and more than double that number in 1900, seem inordinately high. But even with ample allowance for inaccuracy and the reporting of giant catches only, it is evident that far fewer than 6,000 anglers caught as many, or more, perch as are being taken today. Since there may possibly be greater availability of fish in dense populations than there is in those with fewer members (Fry 1949), the large catches quoted for 1900 and 1916 do not seem impossible, even if they are unattainable to the anglers of today.

The increase of anglers on Lake Mendota during this century might be indicated by the population figures of Madison; the city grew from 33,000 to over 90,000 inhabitants between 1915 and 1950. If the numbers of anglers on the lake have increased in the same proportion, or slightly more rapidly because of an increased influx by road of Sunday and holiday anglers, fishing pressure may today be about 3 or 4 times what it was in 1915 and 1916. It is again interesting to note that during this same time the fish increased their average body weight 3.6 times (Table II) and that the only accurate figures at our disposal, namely the gill net catches, illustrate a decline in numbers to about ⅓ of their former abundance. Thus an angler catching 35 to 40 perch in 1916 might have carried home as much in usable proteins as he could secure in 1949 by catching only 10 perch.

It may further be asked whether the present rate of removal of perch from the lake is making a considerable inroad into the existing population. The percentage of various age groups in the winter creels revealed that a yearly mortality of around 50% prevailed among the fish between their 4th and 7th years. This mortality rate is made up of two components; that due to natural death and that which is caused by angling. Assuming that the perch population now consists of around 3,000,000 mature fish from which about 150,000 are removed by summer and winter angling yearly, the harvest by man would be 5% of the stock, or 10% of the total yearly mortality rate. A harvest even twice as large as that can be considered small from a commercial as well as a sport-fishing point of view.

Another indication of the negligible influence of angling on the Mendota perch might be gained from a glance at the period from 1941 to 1945 (World War II). It is reasonable to assume that there were fewer anglers on the lake during that period than either before or after it, even if one were to take into consideration the increased efforts of some householders to make up for meat shortages. If such a decrease in fishing pressure had any effect at all, one would expect it to

have produced increased competition and thus to have depressed the growth rate of the fish. No such effect could be detected.[5]

Conclusion

One might now attempt to evaluate the importance of the environmental influences which were discussed and point out that there were probably other minor ones which could not be properly assessed.

The yellow perch of Lake Mendota during the last fifty years have decreased considerably in numbers. During that period their average size has more than doubled. Thus they have provided an exemplary illustration of the inverse relationship often found to prevail between the number and the size of fish in a body of water.

The figures of average perch sizes and weights calculated from samples taken at various intervals between 1916 and 1948 suggest that years of gradual increase may have alternated with more rapid gains in length and weight (Table III). Unfortunately there are no observations available to permit a similar breakdown of the reduction in the numbers of perch; reliable data exist only from the beginning and the end of the 30-year interval.

The most noticeable acceleration of the growth rate occurred after 1939; in this year the perch disease caused by the myxosporidian *Myxobolus* first reached epizootic proportions. In the following year the cisco, competitors of the perch, died in large numbers; a similar though less severe die-off had already occurred among them in 1932.

The yearly perch epizootics do not reach spectacular proportions any more, they declined in severity after 1946; the parasite, however, is still present in the lake. It is likely that this was its status also before 1939 when it began to affect the perch more seriously. "A lag of one, or even two, years may well occur before the changed severity of the disease finds expression in a somewhat faster, or slower, rate of perch growth. Thus a gradual decline of perch infections in 1947 may not yet have shown up in the sizes of adult fish in 1948.

It has been impossible to show any changes in the amount of perch food in the lake during the years covered in this study. By analogy with other waters it appears that the fertility of Lake Mendota and thus its production of plankton and bottom organisms for perch food should, at least, have kept its level (Hasler 1947). Thus the same amount of food would be present for utilization by increasingly fewer and younger perch with a decrease of competition by cisco into the bargain. It is also known that young fish utilize their food more effectively than old ones (Moore 1941; Pentelow 1939).

The present rate of removal by angling leaves a wide safety margin and appears as a factor of minor importance in the recent population changes. It must not be forgotten, however, that immature fish are rarely taken by anglers who concentrate their efforts on the older, hence larger, perch in the population. It has been shown that yearly epizootics have also preferentially culled the perch from the higher age groups. The severity of the epizootics fluctuated throughout the years and only at times of heavy mortality among the older fish could angling have been a more substantial influence in determining the size of the spawning population than it is now.

Available evidence points to the epizootics of the sporozoan disease as the

[5] To bring this discussion up to date as far as March 1951 the following preliminary report in the winter fishing of the season 1950/51 should be added. The number of perch caught per unit of angling effort did not vary appreciably from the figures of the last 5 years; the average size, however, declined somewhat.

Since we have, as yet, no age group analysis of these catches it is difficult to decide whether we are confronted with a decline in the numbers of perch in the lake where the anglers draw on younger, hence, smaller fish or whether the growth rate of the perch is declining again. In the light of the evidence presented here (the recent ebb in epizootics and the increase in the cisco population of Lake Mendota) the author is inclined to support the latter interpretation.

most important single influence to account for the changes among the perch of Lake Mendota; fluctuations in competition, and changes in the amount of angling throughout the years could have supported to some extent the effects of the disease and allowed the individual fish to grow larger while their numbers were reduced. Additional factors such as the influence of the climate on spawning success during different years and a possible increase in food organisms could not be evaluated because there was not sufficient information about them; both might have tended to accentuate the observed effects.

Summary

A severe reduction in numbers and an increase in the average size and weight of the yellow perch (*Perca flavescens* Mitchill) in Lake Mendota, Wis., occurred during the first five decades of this century.

Fish were removed by angling only during that period in which winter creels were reported to decline substantially. A comparison of catches with experimental gill nets also indicated a decline in the numbers of perch. During the spawning season of 1916 the catch per 100 feet of gill net per hour was 15.5 perch but only 3.6 perch could be caught with the same unit of effort at a comparable time of the year in 1947; this represents a 4.3-fold decrease. In the same time-interval the average total length of adult perch increased from 162 mm. to 243 mm. and the average weight from 50 to 180 grams, or to 3.6 times its former level. This increase numerically almost equals the observed decline in the number of perch. The most rapid changes in size and weight appear to have taken place between 1939 and 1948.

The following factors could be connected with these changes: (a) repeated epizootics leading to fluctuations in the population level; (b) a temporary reduction in the number of cisco (*Leucichthys artedi* LeSueur), probably a competitor for food and space; and (c) fishing pressure. This last factor could only have contributed materially to the observed effects during short periods immediately following the epizootics.

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NOTES AND COMMENT

CONCERNING A RECENT PAPER ON THE INSECTS AND RELATED ARTHROPODS OF ARCTIC ALASKA

Current interest in Arctic ecology would seem to warrant calling attention to a recently published article entitled "A survey of the insects and related arthropods of Arctic Alaska, Part I," by Neal A. Weber (Trans. Amer. Ent. Soc. **76** (3): 147–206, 6 pls., 1950). This contribution is based on field work undertaken by Weber during portions of the summer seasons of 1948, 1949 and 1950 in that part of Alaska from the Brooks Range north to the Arctic coast. Within this region most of the material so far reported came from the localities of Pt. Barrow, Umiat and Anaktuvuk Pass.

Unquestionably much work has gone into this publication and an appreciable increase in our knowledge of the Arctic fauna has resulted. A casual examination of the paper reveals an apparently self-contained, comprehensive treatment of the kind welcomed by the ecologist or student of animal distribution. As indicated by the table of contents there is discussion covering a wide range of subject matter. The reader will be intrigued by such headings as "Origin of Arctic Insects," "Migratory Routes," "Relations of Insects and Plants" . . . etc. In the list of species he will note that records from other published sources have been added, and that many of these records concern species found in Canada, Greenland or Iceland but not known from Alaska. With these considerations in mind some workers may be tempted to accept this publication as a basic reference for future studies. Lest this happen, it seems advisable to point out certain deficiencies which all but negate use of the paper for more than the records of organisms actually collected by Weber.

An examination of the discussion under the general headings reveals little or no new information, whereas remarks compiled from other sources have been abbreviated to the point of becoming elementary generalities. For example, it is said that "Areas in the American Arctic are also believed to have been unglaciated." Even a beginning geology text will reveal that most of the lowland areas of western Alaska as well as the Arctic slope show no evidence of glaciation. The strong probability that this area was at that time connected with Siberia by a continuous land bridge makes the matter one of paramount importance, since a valve-like effect on the distribution of at least certain elements of the fauna and flora of the Palaearctic and Nearctic Regions would have resulted.

At first sight the list of insects and other arthropods is impressive. There are about 430 entries; however, at least 68 are not Alaskan, but are from Greenland, Iceland or even Spitzbergen. One might think that the list is inclusive of all Arctic species, but the only Greenland and Iceland records are those taken from the published studies by Dr. Marie Hammer on mites and Collembola. One remark on page 155 states that "Canadian Arctic records are included when the species is known from Alaska," but exceptions such as *Rhagidis gelida* Thorell on page 159 and *Achorutes armatus* Nicolet on page 169 are noted. In the case of mites and probably also Collembola it was the author's intention to include non-Alaskan records when the species belonged to genera known to be present in Alaska. However, *Platynothrus peltifer* Koch is omitted, although *Platynothrus* sp. is recorded from two Alaskan localities.

If the reasons for the inclusion and exclusion of records from published results of the Canadian Arctic Expedition and those of Dr. Hammer are obscure, neither is it clear why records of the many other workers on the American Arctic should be ignored. Of even greater concern are the considerable number of important papers pertaining directly to Arctic Alaska which have been overlooked. Perhaps the most important of these are three papers published by John Sahlberg in 1885 (Coleoptera och Hemiptera, insamlade af Vega-Expeditionen—Ur. "Vega-Expeditiones Vetenskapliga" Bd. **IV**, pp. 1–42; 45–57; 61–71). In these papers 16 species of Coleoptera and 1 of Hemiptera are reported from the coast of Seward Peninsula. Only one of these species is mentioned in Weber's paper.

On page 178 Weber writes "There is one record of water boatman (*Arctocoriza*) in the Alaskan Arctic and a search should be made for others." Presumably "search" refers to field studies; however, a minimum bibliographic search would have revealed that *Arctocorisa chanceae* Hungerford and *Callicorixa producta noorvikensis* Hungerford were described from specimens collected at Noorvik, Kobuk River (Hungerford, 1926, Ann. Ent. Soc. Amer. **19**: 462).

If purely Icelandic records are included, why are the many records contained in papers concerning the Pribilof Islands not also listed? One of these papers, written by W. L. McAtee, treats the "Apterygota, Anoplura and Heterop-

tera of the Pribilof Islands, Alaska" (North American Fauna, No. **46**, pp. 139–145; Bur. Biol. Survey. U.S.D.A. 1923). Another contribution consists of a series of nine papers by nine authors published under the title "XIV—Insects of the Pribilof Islands, Alaska" (Proc. Calif. Acad. Sciences **11** (14): 153–195, 7 text figs. 1921). This collection of papers treats seven orders and includes records for 86 species. In view of Weber's definition of Arctic Alaska it might also be argued that records from the Aleutian Islands should be included. Certainly few of those islands support coniferous trees, and the inclusion of a record from Mt. McKinley Park serves to strengthen the argument.

Beyond exhibiting an almost consistent absence of either systematic or alphabetized order, the list is characterized by numerous mistakes which would not be expected of a writer having a taxonomic background in entomology. Frequent misspellings may be attributed to faulty proof reading, but many other mistakes seem to have resulted from hasty, uncritical composition. On page 162 three genera are listed under Eupodidae. Of these, *Platynothrus* should be placed with Camisiidae, while *Notaspis* belongs in Notaspididae.

No mention is made of Hemiptera; however, Heteroptera is included as an order. This is contrary to any reference source known to me. Under Homoptera the name Cicadellidae is used for two species of leafhoppers. Then immediately following Coccidae (scale insects) is Jassidae, another family name for the leafhoppers which has not been used in the United States for 30 years.

In Hymenoptera *Vespa* is used in place of *Vespula*, despite the fact that Weber used *Vespula* correctly in his 1949 publication. There is also the observation that cells of a yellow jacket nest contained honey. This should arouse the interest of hymenopterists, since there seems to be no other published evidence that *Vespula* stores honey.

Among the butterfly records, lepidopterists will immediately notice that three species of *Colias* have been duplicated under the obsolete name of *Eurymus*. In Diptera, records for Hydrobaeninae are followed by those under the synonymous name Orthocladiinae. The beginning entomology student who has just classified a chrysomelid beetle as a coccinellid will be pleased to find "Ladybird Beetles" used on page 182 as the common name for Chrysomelidae.

Most of these errors, as well as many others not mentioned here, could easily have been avoided by submitting portions of the manuscript to competent specialists in the various orders.

Judging from his records, Weber devoted a considerable part of his attention to collecting mites and other arthropods contained in soil or in plant debris. Records for higher insects are surprisingly few. No doubt many of these will be reported in the subsequent part or parts. While these records will be welcomed, the need to refer to at least three separately published papers will be a source of inconvenience (e.g., Weber, "Late Summer Invertebrates, Mostly Insect, of the Alaskan Arctic Slope," Ent. News **60**: 118–128; Weber, 1950, Part 1; Weber, [subsequent parts]).

Perhaps the shortcomings of the paper under consideration represent the result of trying to cover too large a field in too short a time, combined with premature publication. Whatever the reason, students of ecology or animal distribution should not accept more of this paper than the list of insects and other arthropods actually collected by Weber.

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FOREST DEVELOPMENT FOLLOWING GLACIER RECESSION OBSERVED IN 1776

The following quotation is from: "Sketches of the Natural, Civil, and Political State of Swisserland; in a series of letters to William Melmouth, Esq. from William Coxe, M. A., Fellow of King's College, Cambridge; and Chaplain to His Grace the Duke of Marlborough," second edition, London, 1780. (The first edition was published in 1778. The letters were written in 1776.)

Pages 247–250. (Comments about a visit in 1776 to the Montenvert, and to the glacier, most probably the Mere de Glace, but possibly the Bosson, or both, of Mont Blanc.)

"I cannot conceive any subject in natural history more curious than the formation and progress of these glaciers; running far into fields of corn and rich pasture, and lying, without being melted, in a situation where the sun has power sufficient to ripen the fruits of the field: it is literally true, that with one hand we could touch ice, and with the other ripe corn. But, as this is a subject too important to be treated superficially, and requires much accurate observation, and repeated experimental investigation; I shall not attempt to enter into it. I will beg leave nevertheless to trouble you with one obser-

vation, which I made: and it will serve to prove the occasional encrease and diminution of the glaciers; contrary to the opinion of some philosophers, who advance that they remain always the same; and of others who assert, that they are continually encreasing. I think I may venture to assert, that both these positions are equally untenable; and it happens in this, as in many other subjects, that experience and truth are sacrificed to the supporting of a favorite hypothesis. Indeed the fact seems to be that these glaciers in some years encrease considerably in extent, while in others they recede; and of this I am perfectly convinced from the following circumstances:

"The borders of the valley of ice of the glacier of Montenvert, are mostly skirted with trees: toward its foot a vast arch of ice rises to near an hundred feet in height; from under which, the continued droppings from the melting of the ice and snow are collected together, and form the Arveron; which rushes forth with considerable force, and in a large body of water. As we approached the extremity of this arch, we passed through a wood of firs; those which stand at a little distance from the ice are about eighty feet high, and are undoubtedly of a very great age. Between these and the glacier, the trees are of a later growth; as is evident as well from their inferior size, as from their texture and shape. Others, which resemble the latter, have been overturned, and enveloped in the ice; in all these several trees, respectively situated in the spots I have mentioned, there seems to be a kind of regular gradation in their age, from the largest size to those that lie prostrate.

"These facts fairly lead, it should seem, to the following conclusions:—that the glacier once extended as far as the row of tall firs; that, upon its retiring, a number of trees have shot up in the very spots which it formerly occupied; that, within some years, the glacier has again begun to advance; and in its progress has overturned the trees of later date, before they have had time to grow up to any considerable height.

"To these circumstances, another fact may be added, which appears to me convincing. There are large stones of granite, which are found only at a small distance from the extremities of the glacier. These are vast fragments, which have certainly fallen down from the mountains upon the ice; have been carried on by the glacier in its encrease; and have tumbled into the plain upon the melting or sinking of the ice which supported them. These stones, which the inhabitants call *Mareme,* form a kind of border, towards the foot of the valley of ice, and have been pushed forward by the glacier in its advances; they extend even to the place occupied by the larger pines."

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DESTRUCTION OF FISHES AND OTHER ORGANISMS ON THE SOUTH TEXAS COAST BY THE COLD WAVE OF JANUARY 28–FEBRUARY 3, 1951

Introduction

The South Texas Coast in the general region of Corpus Christi is at the same latitude as Tampa, Florida. Cold polar fronts push as far south here as at any place on earth. These are the well-known Texas northers of fact and story. Occasionally they are strong enough to cross the Gulf of Mexico and over the Isthmus of Tehuantepec down to Nicaragua on the west side.

Texas has approximately 3,500 square miles of bay waters. These waters are shallow, the average offshore depth being 6 to 8 feet. The bays are connected with the Gulf of Mexico by relatively narrow passes, there being only five of any size along the 360 miles of shoreline. Due to these physiographic features and the extremely rapid onset of the northers, accompanied by sharp drops in water temperature, occasionally mortalities of marine life are caused. Gunter (1941, 1945) has recorded instances. In some cases destruction attains catastrophic proportions. Observations throughout the years have indicated that the amount of destruction depends on several things beside the low temperature attained.

In this paper the writers wish to describe the effects of the cold wave of January-February, 1951, in and around Aransas Pass, one of the major passes of the Texas Coast. It lies about 21 miles due east of the city of Corpus Christi, and 130 miles north of Mexico.

Data

On January 28 the norther struck at about 5 o'clock in the afternoon. It came in gradually and temperatures dropped slowly that night. The wind slowly increased next day and the next night, attaining a speed which varied from 25 to 40 miles an hour. Temperatures dropped below freezing on January 29 and remained below freezing for five days. The minimum temperatures recorded at the Corpus Christi Weather Bureau station from January

29 to February 3, in consecutive order, were: 25, 22, 22, 18, 20 and 19° F. In the citrus belt of the Rio Grande Valley, 125 miles to the south, temperatures fell to a little below 19° F. and extensive damage was done. Ranchers reported some losses of cattle but these were not severe. In length of time the cold held on and the low temperatures attained, this cold spell compares only with the great freezes of 1890 and 1882 on the South Texas Coast. Along the lower parts of the coast it broke all previous records.

We noted four brown pelicans dead and heard reports of others. White pelicans are quite common in this region in the winter but no dead ones were heard of or seen. One dead Caspian tern was seen. On January 31 a common loon, *Gavia immer,* was found on the Gulf beach in a helpless condition and covered with ice. It was released on February 3 and swam away. Four myrtle warblers, *Dendroica coronata,* and one bluebird, *Sialia sialis,* were found dead during and after the freeze. They probably starved as well as froze, for the ground and all plants were covered with ice.

On February 9, one week after the freeze, a large leather-back turtle, *Dermochelys coriacea,* drifted ashore in the northwest part of Copano Bay at the town of Bayside, Texas. This turtle was a male measuring 6 feet and 8 inches long from nose to tail and was estimated to weigh around 500 pounds. This is a tropical species not particularly common anywhere and so far as we know this is the first written record from the Texas Coast, although it is not unknown to native fishermen. Possibly it died from natural causes but it seems strongly coincidental that an uncommon turtle of this size should come ashore right after the hard freeze.

The writers made notes on the fishes killed by examining the Gulf shore of Mustang Island for a distance of 3 miles, the south jetty of Aransas Pass, the shore of the ship channel leading to Aransas Pass, the harbor in the city of Aransas Pass, the northern shore of Aransas Bay along Live Oak Peninsula and the southern shore of Copano Bay along the same peninsula. Examinations of the Gulf beach and the jetties were made on February 1 and 2. Examinations of Aransas Pass harbor and Aransas and Copano bays were made on February 2 and 4. Some observations were made on the north shore of St. Charles Bay on February 4 and on the north shore of Copano Bay on February 10.

The fishes on the Mustang Island beach consisted almost solely of the hardhead catfish, *Galeichthys felis.* It was estimated that approximately 6,000 catfish lay along the beach over a distance of a mile and a half south of the jetty. South of that point they were scattered with only a few fish every 100 yards. The following dead fishes were also noted along this beach: the anchovy, *Anchoa mitchelli diaphana;* needle-gar, *Strongylura marina;* butterfish, *Poronotus triacanthus;* silverside, *Menidia beryllina peninsulae;* black drum, *Pogonias cromis;* yellowtail, *Bairdiella chrysura;* pinfish, *Lagodon rhomboides;* spiny boxfish, *Cyclicthys schoepfi;* and an unknown conger eel.

Along the jetties there were numerous catfish, a few speckled trout, *Cynoscion nebulosus,* a few drum, *P. cromis,* and a number of sheephead, *Archosargus probatocephalus.* The numbers ranged from 3 to 10 per yard. The yellowtail, *B. chrysura,* and the pinfish, *L. rhomboides,* numbered about two each to the yard. Anchovies dead and dying were present in large numbers. One cyprinodontid, *Fundulus similis,* was found alive but stranded. Closer gleanings for smaller fish in a short distance yielded a sea robin (*Prionotus*), three seahorses (*Hippocampus hudsonius*), one midshipman (*Nautopaedium porossisimum*), six graysnappers (*Lutjanus griseus*), one mullet (*Mugil cephalus*), two *P. triacanthus,* one needlegar, ten *C. schoepfi,* two butter hamlets (*Hypoplectrus unicolor*), one worm eel (*Myrophis*), and 18 Louisiana pipefish (*Syngnathus louisianae*).

The ship channel leading into the city of Aransas Pass had black drum and speckled trout scattered along the shores. People were picking up trout. Some had collected as much as three bushels. Several hundred dead anchovies were seen in one spot. Nevertheless, on the whole few cold-killed fishes were seen along this channel.

On February 2 in the Aransas Pass harbor a few hundred people were fishing along the shores with ordinary casting rods and 3-pronged hooks or grabs instead of the usual bait. They hooked onto the dead and inactive trout and several large catches were made. Fish were also taken in dip-nets or merely raked in with oars. Several people made catches amounting to 40 or 50 pounds. Most of these fish appeared not to be dead but merely in a stunned or inactive condition. Numbers of them probably would have survived. The shores of the harbor at this time were lined with a good many pipefish, pinfish, ribbonfish (*Trichiurus lepturus*), croakers (*Micropogon undulatus*), and flat croakers (*Leiostomus xanthurus*). On February 4 the shores were lined with a much greater number of small dead fishes. Their numbers amounted to approximately 30 per yard. A count along one yard of the shore showed 24 *L. rhomboides,* 2 yellowtail (*B. chrysura*), 2 striped mullet (*Mugil cephalus*), 1 silverside (*M. b. peninsulae*), and 1 flat croaker (*L. xanthurus*).

The north shore of Aransas Bay yielded little fish during either examination. At the time of the cold wave it was a lee shore and fish would have drifted to the south. However, considerable numbers of mullet, speckled trout,

sheephead, black drum and redfish later drifted to shore on this bay north of Fulton. Large strips of mush ice were seen on some of the shores of the offshore islands on February 2.

Dead fishes were not present on the shores of Copano Bay in spectacular amounts on February 2. However, closer examinations showed that in some places great numbers of anchovies, *Anchoa mitchelli diaphana,* were present. Other fishes seen were croakers, yellowtail, sheephead, the hake (*Urophycis floridana*), the small eel (*Myrophis punctatus*), the shad, (*Signalosa mexicana*), the naked goby (*Gobiosoma bosc*), pinfish, puffers (*Sphoeroides*), stargazer (*Astroscopus*), and striped mullet. Larger fishes continued to come ashore up to three weeks after the freeze. These were trout, redfish and drum. On February 10 the exposed tidal flats on the north shore of Copano Bay showed considerable numbers of speckled trout, striped mullet, black drum and gizzard shad (*Dorosoma cepedianum*).

Few fish were seen along the shores of St. Charles Bay although large numbers were reported to be floating in the middle of the bay.

Examinations of parts of Karankaway Bay, Matagorda Bay and the Laguna Madre were made three weeks to a month later. Fish carcasses, especially the larger ones, were still much in evidence. Thousands of mullet were seen and possibly more of this species were killed than of any other fish. In some shallow ponds near the bays the cyprinodontid, *Cyprinodon variegatus,* were wiped out.

Considerable numbers of invertebrates were observed along the shores of Copano Bay. There were thousands of the little flat crab, *Petrolisthes armata,* and a considerable number of blue crabs, *Callinectes sapidus.* Commercial shrimp, *Penaeus aztecus,* and spider crabs were also observed. The snapping shrimp, *Crangon,* was very abundant. Two dead squid, *Loligo brevis,* were seen. Along the Gulf beach one *Penaeus aztecus* and two molluscs were the only invertebrates seen. One of these was the gastropod, *Phalium granulata,* and the other was the pelecypod, *Noeta ponderosa.* Following the cold spell oyster tongers brought up large numbers of stone crabs, *Menippe mercenaria,* in an inactive condition among the tong loads of oysters. Windrows of commercial shrimp, *Penaeus aztecus,* were reported on the islands of lower Aransas Bay, but were not observed by us.

After the freeze several pictures of dead fishes in the Laguna Madre were published in the papers. Here the fish were piled up in windrows several hundred yards long. These extended for a distance of some thirty miles along the upper Laguna shore. Damage was less in the lower Laguna. Figure 1 is a series of pictures of fishes killed in the Laguna Madre. They were taken by marine biologists of the Texas Game, Fish and Oyster Commission, to whom we are indebted for permission to use them.

Discussion

There are a dozen or more papers reporting mortality of marine organisms caused by cold in Florida, Texas, the Bermudas and Denmark. References not previously cited in the papers referred to above are: Blegvad (1929), Johansen (1929), Smidt (1944) and Verrill (1901).

There is no doubt that the fishes and other animals reported in this paper were killed by the cold. Numerous others were inactivated and rendered temporarily helpless. It further seems clear that, although several million fish were killed along the Texas Coast by this record-breaking cold wave, the destruction of marine life was not more severe than the spell of 1940 previously reported (Gunter 1941). In our opinion it was less. In addition to our own observations, we checked with six game wardens and commercial fishermen. Opinion ran 5 to 1 that the 1940 freeze was more damaging to marine life. The cold spell of 1947 also did considerable damage according to all general reports. The cold wave of 1949 caused less destruction to marine life. It went unrecorded in the literature except for reference to destruction of certain elements of the chaparral on land (Gunter 1950).

A comparison of observations by the senior author during the two spells indicates that mortality was greater in Copano Bay, Aransas Bay, Aransas Pass and along the Gulf beach during the 1940 freeze. Following the 1940 cold wave windrows of dead fishes were present in the Laguna Madre and also down the Mexican Coast. During 1940 the temperature of the open bay fell to 39° F. and there was considerable ice along the shore. During 1951 the lowest temperature reported in the open bay was 38° F. and there was also considerable ice along the shores. Although the air temperatures in 1951 were considerably lower, the cold did not remain any longer than in 1940 and the water temperatures were about the same during both spells. Marine biologists of the Game, Fish and Oyster Commission estimated in newspaper reports that 60 to 90 million pounds of fish were killed in 1951. Exact estimates are difficult, but there is no doubt that destruction was enormous.

This raises the question of why some cases of mortality are more severe than others, although the low temperatures may be nearly the same or may even fall lower in cases of lighter mortality. Storey and Gudger (1936) and Gunter (1945) noted that, for one thing, the destructiveness of cold waves depended upon the rapidity of the temperature drop more than upon the low attained. The facts seem to be

explicable on the basis of acclimatization. A comparison of the 1940 instance and that of 1951 yields the following information: In 1940 the cold spell was the first hard one of the season. It came on with extreme rapidity and air temperatures fell from 65° to 25° F. in four hours. The damage to fishes was enormous and was great enough to bring about a reduction of the commercial catch during the following year. In the winter of 1950–51 one cold spell brought freezing temperatures to the Texas Coast during the first part of December. Another freeze followed on January 6. These did not cause any mortality but could have caused many animals to leave the bays. The cold wave of 1951 came on gradually and there was one night without freezing temperatures. The air temperatures over the water fell to approximately 18° F. Thus, in 1951 the fishes might have been acclimatized by the previous cold spells and also affected comparatively less by the slow onset of the major one. Similarly, large numbers of them might have been forewarned by the same two factors and thus have made their escape to deeper and warmer waters. One of us (Gunter 1945) has previously shown that there is a cyclic movement of fishes and other marine animals from the bays into the Gulf of Mexico which starts every year at the onset of cooler temperatures in the fall. Party boat fishing for sea trout and redfish in the bays had practically ceased in January, 1951,

FIG. 1. (*Continued on facing page.*)

FIG. 1. Fishes killed in the Laguna Madre of Texas by the cold wave of January 28–February 3, 1951 (Photographs by courtesy of the Game, Fish and Oyster Commission.)

because the fish had largely left the bays. In any case, it seems to be clear that the amount of damage to marine life on the Texas Coast is dependent upon the rapid onset of northers as well as the degree of low temperature attained. Whether or not the damaging northers have been preceded by other cold waves is also a factor influencing the amount of mortality.

The marine life of the Texas Coast and the west coast of Florida seem to be particularly subject to destruction by hard cold spells. Gunter (1947) considered this matter in connection with catastrophic mass mortalities in the sea and the increased chance for fossilization. Nevertheless, the Recent deposits along the Gulf yield very few fossils, although the northers and other agents producing catastrophic mortalities of fishes must have been operative in this environment for 25,000 years or more.

The physiographic features of the Texas Coast and the quick onset of the northers explain to some extent the prevalence of fish kills in this region. The presence of large numbers of fishes with tropical affinities also plays a part as Storey (1937) has postulated for Florida waters. Her paper showed conclusively that mortality was most extensive among those fishes with tropical distribution.

Summary

The shallowness of Texas bay waters, their practically landlocked condition and the rapidity with which cold northers strike the coast are factors making the marine life of this area particularly subject to mortality from cold waves every few years. Since 1940 slight mortality was caused by cold waves in 1941 and 1949. Considerable damage was caused in 1947. The 1940 and 1951 episodes were catastrophic. Probably the 1940 instance was the most severe although the 1951 freeze was the hardest. Estimates made by biologists of the Game, Fish and Oyster Commission of the amount of fish killed in 1951 range from 60 million to 90 million pounds. It seems that if the damaging cold waves are preceded by other freezes, their destructive effect is lessened. Some animals escape to deeper water if the onset of the cold wave is slow and the rapidity with which the northers strike is a factor influencing the amount of mortality.

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ECOLOGICAL LIFE HISTORY OUTLINES FOR FUNGI [1, 2]

Introduction

This is another in the series of outlines and bibliographies of ecological life history studies of both plants and animals which are currently appearing in Ecology, under the sponsorship of the Committee on Ecological Life Histories.

The study of mycology and its related subjects including plant pathology, human pathology, and the various fields of industrial microbiology devoted to the study of various aspects of fungus physiology, has resulted in a high degree of development in ecological life history studies in this particular area. As in parasitology this group is far ahead of any other group of organisms in life history studies because of the facility of culture of saprobic species, and because of the great economic importance of saprobic, perthogenic and pathogenic species. Ecological life history study methods have been in use in the above mentioned fields for a long time to solve practical problems of disease control in crop plants including forest trees, in domestic animals and man, as well as practical problems in the manufacture of industrial alcohol, antibiotics, various chemical compounds, and the prevention of decay in various organic materials including natural and synthetic fibers and other products. This group of organisms has thus been in a most favorable position to compete for attention and funds for research on and development of our knowledge of their ecological life histories. The result of this interest is a vast literature on methods of study and life history monographs which are rarely complete but are usually devoted to one or more phases of the life history of the organism, especially those associated with the practical problem at hand. Within the fungi there is a great diversity of ecological relations, basic physiology,

[1] This investigation was supported in part by funds provided for biological and medical research by the State of Washington Initiative Measure No. 171.

[2] Scientific Paper No. 1031, Washington Agricultural Experiment Stations, Institute of Agricultural Sciences, The State College of Washington, Pullman.

morphology, cytology and genetics; this makes the preparation of a general outline for study a very complex problem, since all phases of the biology of the organisms are not studied by a single worker because of limitations on time and funds.

Whether we assume with Bessey (1950) that the fungi are derived polyphyletically by reduction of various functions from higher plants, or whether we assume with Martin (1950) that the fungi arose monophyletically from non-pigmented flagellate organisms, the fungi are studied by workers as a separate group of organisms which follow the same biophysical and biochemical laws as other organisms, whether plant or animal, but in a different way.

Since fungi cannot manufacture their own food they must rely on other organisms for food sources. Thus we have, according to Ehrlich (1941), three principal groups of fungi according to their food sources. The terminology used follows the ideas presented by Rogers (1948) and Martin (1950). *Saprobic* fungi derive their food from dead organic matter; *perthogenic* fungi derive their food from dead parts of living plants; *pathogenic* fungi derive their food from living parts of living plants, animals or fungi. There are *obligate pathogens* which cannot be grown in pure culture but must spend their entire life cycle in association with living host tissues; and there are *facultative pathogens* (or *facultative saprobes*) which live for part of their life cycle in living host tissue but for the remainder of their life cycle on dead host tissue. These latter organisms, as well as true saprobes and obligate and facultative perthogens, can be cultivated throughout the whole life cycle in most cases.

Because of their different biologies the obligate pathogens are studied by different techniques than are the facultative pathogens or the saprobic fungi. The outline for the pathogens is based on a heteroecious rust but can be adapted for studying any obligate pathogen in any class of fungi, such as rusts, downy and powdery mildews, parasites of aquatic fungi and algae, and other fungi, none of which have to date been brought into pure culture on inorganic or organic non-living media.

In nature, saprobic fungi may thrive on a wide variety of substrata or they may have specific narrow requirements. The student of any particular life cycle must bear this fact in mind, for the media or medium to be selected for growing the organism is usually based on these requirements. Many fungus habitat restrictions include: special types of manure; types of thermal habitats such as compost heaps; animal remains such as hair, feathers, hooves, horn and bones; plant remains of various kinds either of lignin or cellulosic composition or both. While certain perthogenic fungi do not continue growth after the host plant dies or the host tissue is removed from the host plant, others, such as many heart-rot fungi of interest to forest pathologists, continue to grow and produce fruit bodies as long as there is suitable food available in the decaying tissue. These species can be studied in pure culture from a number of different points of view, thus obtaining a wide knowledge of the biology of the organism. The literature of forest pathology is replete with studies of various species of forest pathogens. Most of these studies are based on certain phases of the life cycle such as those phases of special interest to the forester, rather than on the complete life history. This statement is true of most life history studies available to students of fungi in the literature. However, for a fairly complete life history study of a fungus of considerable economic importance see Voorhees (1942).

Fungi pathogenic on insects, such as members of the Cordyciptaceae, Laboulbeniales, and Septobasidiaceae, are apparently obligate parasites and have not been studied to any extent physiologically, although recent workers (Fawcett 1944) have become interested in the control of insect parasites of plants by their own diseases. Fungi associated with ants and termites have been recently reviewed (Uphof 1942), those associated with scale insects have received monographic treatment by Couch (1938), and Steinhaus (1946) has recently brought together a large amount of material concerning microorganisms, including fungi, associated with insects.

Fungi pathogenic on higher animals and on man (Emmons 1940, Conant 1944, Nickerson 1947, Skinner, Emmons and Tsuchiya 1947) can be grown in culture away from living tissues and in such instances assume forms entirely different from those in which they are found in histological examination of diseased tissues. The attempt to identify these fungi exclusively by their reactions to pure culture techniques used in standard isolation practices is not always valid. While this simulates the methods of experimental taxonomy, it was through experimental taxonomy dealing with a series of monosporous isolates in several species of Fungi Imperfecti (to which general group most animal pathogens belong) that the "dual phenomenon" (Hansen 1938) was discovered. In its simplest form the "dual phenomenon" applies to the condition in which at least three strains of a species can be obtained from a single spore culture; two of these strains are opposite in certain characteristics, one is intermediate. Continued work with the intermediate can give the three forms. Pairing the opposites can give rise to the original or intermediate strain. No sexual process is known to occur, but a plasmogamy is initiated by anastomoses between spores or hyphae of the strains involved. The spores contain

more than one nucleus. Wilhelm (1947) has shown that in such human pathogens as dermatophytes the "dual phenomenon" plays an important role and may be responsible for the large number of "species" described in the group.

Another group of fungi pathogenic on animals is represented by the Zoopagaceae and its physiologic (if not morphologic) relatives. These organisms live in the soil and attack primitive soil protozoans which they trap and digest. Their biology is not completely known but problems concerning them are indicated in at least one of numerous papers (Dreschler 1948) recently presented.

A number of specialized groups of saprobic fungi can be indicated. The study of the fungi involved requires certain special techniques, and again the students of these fungi are interested in special problems. Under certain conditions a number of fungi grow on wood submerged in ocean water (Barghoorn and Linder 1944). A number of species of fungi commonly found on decaying plant materials are of considerable importance in the pulpwood industry (Goidanich 1938, Björkman 1949). These and other fungi are of importance throughout industry and medicine as laboratory contaminants, as producers of allergy, as producers of important chemicals, and in other ways (Smith 1946, Thom and Raper 1945, Raper and Thom 1949).

In industry the production of industrial alcohol is of great importance. The most important fungi in this process are yeasts. A large amount of work has been done on the physiology of these fungi, especially in relation to the production of alcohol. Lindgren (1949) has studied these specially from the point of view of the physiologic genetics of the organisms.

In agriculture a most important group of fungi is that which inhabits soils. These fungi decompose organic matter and are of considerable importance in the nitrogen cycle. The work of Chesters (1949), Feher (1933), Gilman (1945), and Kubiena (1938), indicates some of the complexities of this problem.

The following outline for saprobic fungi is based in part on the ecologic life history outline suggested by the British Ecological Society (1941). The form roughly follows that used by Pelton (1951) in this series. It has been modified for the fungi as various phases of the life cycle have become evident through a brief survey of the literature. The accompanying bibliography has been selected in part for emphasis of certain phases of the life cycle, in part for presentation of review articles with as wide a selection of supplemental bibliographies as possible. In addition to information obtained from special and review articles, the following texts are a great source of information (Heald 1943, Baxter 1943, Foster 1949, Bessey 1950).

Outline I. Myxomycetes [3]

1. Spores.—*Longevity.*
2. Spore germination and primary development.—*Germination:* in relation to moisture, temperature, mineral nutrients; method of germination; number of swarm cells produced; possibility of necessity of proximity to enzymes, *i.e.*, ability to produce own enzymes or dependence on other organisms for such substances. *Swarm cells:* flagellation; nuclear condition; environmental factors; fusion or aggregation; formation of myxamoebae. *Myxamoebae:* flagellation; method of locomotion; habitat requirements; food source; fusion, aggregation; formation of plasmodium. *Nutrition of myxamoebae and plasmodium:* method of obtaining food: ingestion of concrete particles including inorganic and organic matter, bacteria bodies and mold spores, use of food substances in solution; necessity for presence of bacteria and molds; types of food used, types of organic and inorganic materials required.
3. Fusion of swarm cells and development of plasmodium.—*Fusion:* of swarm cells a karyallagic rather than a sexual phenomenon. (According to Link (1929) karyallagy refers to a nuclear phenomenon and is applicable here according to Martin because there is no accessory structure associated with the concept of sex present in this group of organisms.) *Formation and development of plasmodium:* formation by aggregation of many myxamoebae, by growth of single myxamoeba, or by intermediate condition; elimination of competition by ingestion; nature of gelatinous membrane surrounding naked protoplasm; nuclear phenomena: simultaneous nature of mitosis in a plasmodium, degeneration of unfused or undivided nuclei; conditions of growth through rhythmic streaming of protoplasm within the mucilaginous sheath, fate of sheath as growth advances the plasmodium; growth of plasmodium affected by: positive or negative phototropism, geotropism, rheotropism, hydrotropism, thermotropism and chemotropism; differences between myxomycete protoplasm streaming and that which occurs in fungi and higher plants, similarities with that of rhizopods; composition of gelatinous membrane or "plastin," of spore wall "cellulose" or more probably myxoglucosan,

[3] This outline follows closely the review by Martin (1940). It is generalized and no attempt is made to include exceptions within or outside the scope of the review article. The outline is a synthesis of conditions in a number of species and genera. For another type of slime mold life history see Raper (1941) on *Dictyostelium* in the Acrasiales.

of capillitium proteinaceous. *Sclerotia:* formed under adverse environmental conditions; germinate to form myxamoebae.

4. Development of fructification.—*Stimuli:* probably exhaustion of nutrients but other possibilities considered include: desiccation, nature of substratum, acidity, light, injury, a type of mystic growth rhythm; pigmented plasmodia require light for initation of fruiting; capillitium formed of waste products or exudates, originates through vacuoles. *Spore formation:* cleavage of cytoplasm; simultaneous meiotic divisions (in most cases); development of spore walls and markings from cytoplasm. *Spore discharge:* by mechanical rupture of sporangium wall; dissemination by air movement.
5. Destruction of fruit bodies.—In some cases by molds in wet weather; bacterial action.
6. Habitat.—*Plasmodium:* within rotting logs, litter, soil and on bark of trees. *Fructification:* on surface of similar substrata.
7. Communities.—Collection of slime molds in nature in association with other species of slime molds is rare.
8. Biotic interrelationships.—Plasmodia feed on fleshy fungus fruit bodies as well as decaying organic matter; fructifications occur on whatever substrata are available for support; bacteria appear to be important in initial stages of development; bacteria, molds and mold spores serve as food for plasmodium as may minute protozoa, myxamoebae and other plasmodia in immediate vicinity.
9. Reactions to habitat as evidenced by fruit body production.—In limestone regions there is a predominance of species forming calcareous deposits in capillitium; favorable habitats result in increased number and size of fruit bodies.
10. Phenology.—Studies needed in nature; present data from collection records only; fruiting can be obtained in laboratory by manipulation of environmental factors in culture chambers.
11. Parasites and diseases.—In wet weather and unfavorably moist habitats fruit bodies are attacked by a number of molds; in nature, except when fruiting, plasmodia are hidden and this problem has not been studied to any extent.
12. Geographic distribution.—Many species cosmopolitan—of world-wide distribution, few are restricted to one or a few localities; in general species with calcareous deposits in fruit bodies occur in limestone regions or tropics, species without such deposits occur in temperate regions and sandstone areas although this is only a tendency indicated by literature reports.
13. History.—Known and studied for over 200 years.

Outline II. "Water Molds"[4]

1. Spores.—*Longevity. Zoospores:* motility, number of flagella per zoospore, nuclear condition. *Gametes:* motility, number of flagella; *male:* size, pigmentation; *female:* size, lack of pigmentation; isogamy. For development of gametes see Hatch (1935); for structure of gametes see Hatch (1938).
2. Germination.—*Resistant sporangia zoospores:* germinate to produce gametophyte mycelium; *thin-walled sporangia zoospores:* germinate to produce sporophyte mycelium; *gametes:* fuse to form planozygotes; *planozygotes:* exhibit amoeboid movement; germinate with germ tube from ameboid structure to form sporophyte mycelium; conditions and method of germination of zoospores and gametes. For details of conjugation process and zygote formation see Hatch (1938). In another bisexual water mold, *Achlya,* Raper (1951) has shown that a complex *hormonal system* is associated with the development of the antheridial and oogonial organs and their products.
3. Mycelial development.—*Cell wall:* chitinaceous rather than cellulosic; *nuclear condition:* coenocytic with large central vacuole surrounded by multinucleate protoplasm next to cell wall; protoplasm streaming at growing point, in mature mycelium; *cross walls* usually formed only below zoosporangia gametangia, and at points of injury; *hyphae:* superficial mycelium wide, dichotomously branched; submerged mycelium rhizoidal, irregularly branched, narrow; sporophyte mycelial branches terminate in single or paired thin-walled sporangia, or single resistant sporangia; gametophyte mycelial branches terminate in pairs of gametangia, usually male below female.
4. Maturation.—*Resistant sporangia:* production of resistant sporangia associated with temperature conditions (Jones 1946); cleavage of cytoplasm into zoospore units; break of outer wall; development of papillae in inner wall; passage of resistant sporangia zoospores into culture medium. *Thin-walled*

[4] A life history of a "water mold" (Phycomycetes) based primarily on species of the subgenus *Euallomyces* of the genus *Allomyces* as described by Emerson (1941) with additions based on research with other "water mold" organisms. It should be remembered that in the case of "water molds" the water in which they live need not be a deep lake but may be only a thin film of water in the soil or on any substrate on which the organism is found.

sporangia: cleavage of cytoplasm into zoospore units; development of papillae in sporangium wall; passage of zoospores into medium. *Gametangia:* cleavage of cytoplasm into either male or female gametes; determination of sex and development of gametangia; development of papillae in gametangium wall; passage of gametes into medium.

5. Destruction of fruit body.—Sporangia collapse on discharge of zoospores or gametes; cf. parasites.
6. Habitat.—Isolated only from moist soils.
7. Communities.—A member of the soil mycobiota which to date has been analyzed quantitatively for amount of activity, qualitatively for presence, but not sociologically.
8. Biotic interrelationships.—Unknown, except as host to certain parasites.
9. Reactions to habitat as evidenced by fruit body production.—Problem not studied in nature; in culture all stages are produced easily on a variety of organic media; Kubiena (1938) indicates that in some cases size of fruiting body is modified by pressure from particles of soil, as is shape.
10. Phenology.—Life cycle reproducible at will in laboratory from soil isolates. Hatch and Jones (1944) showed that on revival of air-dried resistant sporangia sexual or asexual zoospores are produced in varying ratios, depending on length of time dried and richness of nutrient.
11. Parasites and diseases.—Not known beyond joint isolation in culture by chance from soil; such genera as *Catenaria* (Couch 1945) and *Olpidiopsis* (Karling 1943) are known to include obligate parasites of mycelial soil "water molds."
12. Geographic distribution.—World wide in moist temperate and tropical soils.
13. History.—Genus discovered in 1911; sexuality postulated in notes in 1918, sexuality described in 1929.

Outline III. Saprobic and Facultative Pathogenic Fungi

1. Spores.—*Viability* in relation to:—altitude (Stakman and Christensen 1946); prolonged desiccation (Fischer 1936); temperature extremes (Buller 1909:126); lyophilization (Raper and Thom 1949, Thom and Raper 1945, Fennell, Raper and Flickinger 1950); submersion in oil (Stebbins and Robbins 1949); depth in soil (Burgess 1950).
2. Spore germination.—In relation to media required (Fries 1943), temperature, moisture, humidity, light (Togashi 1949, Fries 1941, 1943, Snow 1949); requirement of presence of other organisms (Fries 1943); nuclear phenomena (Sass 1929); physiology (Gottlieb 1950); time of dicaryon establishment. Because of moisture conditions Boughey (1949) indicates that incidence of fungus occurrence may be based on these factors: powdery mildews more prevalent in dry habitats, fungi imperfecti parasitic on plants in moist habitats.
3. Primary mycelium [5] (Hein 1930).—Nutrient requirements (Fries 1948, Sinden, Mix and Siu 1948), mineral nutrition (Steinberg 1939, 1950, Perlman 1949, Foster 1939), temperature—maximum, minimum, optimum (Togashi (1949) lists more than 1,000 species of pathogenic fungi with data from more than 1,200 cited references on temperature relations in controlled experiments and in natural conditions), moisture requirements; area occupied by mycelium: in nature, period of time in culture, rapidity of growth; conditions of mycelium during freezing of substratum in nature; changes produced in artificial or natural media (Sinden, Mix and Siu 1948, Lockwood and Reeves 1945); changes in pH, changes in nutrients (chemical composition of medium), substances added to nutrient solution or medium by fungus (Lockwood and Mayer 1938, Lockwood and Reeves 1945, Thom and Raper 1945, Raper and Thom 1949, Lindegren 1949), substances added to nutrients by experimentation to increase growth efficiency (Robbins and Kavanagh 1942, Fries 1948); development of rot or decay in wood (Baxter 1943, Boyce 1938, Hirt 1928, Mounce 1929, Rhoads 1948, White 1919, Haddow 1938, Hilborn 1942); development of mycorhizae (Fries 1941); development of sclerotia and rhizomorphs (Lohwag 1941); longevity.

   Asexual reproduction.—Production of conidia, oidia, blastospores and other asexual means of reproduction of the fungus (Skinner, Emmons and Tsuchiya 1948); relative importance of asexual reproduction methods (Anderson and Rankin 1914, Arx 1949, Heald 1943), numbers of spores produced; temperature, humidity, moisture, light conditions; *dispersal:* conditions of spore discharge and methods of spore dissemination: animals, water, wind; environmental influences on conidiospore production in soil (Kubiena 1938): crowding, dwarfing by soil particles, temperature, moisture, humidity, light conditions, comparative numbers of spores produced in soil.
4. Secondary mycelium.—*Initiation of dual phenomenon* (Hansen 1938, Wilhelm 1947) and subsequent development of Fungi Imperfecti: Introduction of second mycelium: single spore culture—by manipulation, multiple spore culture—natural reaction in nature or laboratory; compatibility (Hansen

[5] Skip in case dicaryon formed prior to or during germination of asco- or basidiospore.

1938, Zuck 1946); anastomosis formation between spores or mycelium; mixture of protoplasm in monocaryotic or coenocytic cells to form coenocytic cells; continuation of heterocaryotic cells throughout subsequent development; vegetative spread of mycelium: area involved, speed of development; development of chemical by-products (Lochwood and Reeves 1945); use of nutrient materials (Lindeberg 1944, Sinden, Mix and Siu 1948, White *et al.* 1948); source of nutrient materials (Lindeberg 1944, Fries 1938, White *et al.* 1948, 1949, 1950); respiration of fungus mycelium (Darby and Goddard 1950, Scheffer and Livingston 1937); development of conidiophores in relation to temperature, moisture, humidity, light; chromosome numbers; development of pigments (Raper and Thom 1949, Thom and Raper 1945, Higinbotham and Powers 1947); changes in culture medium (Lindeberg 1944, Sinden, Mix and Siu 1948): nutrients withdrawn from medium by fungus, substances added to medium by fungus (Lockwood and Reeves 1945), *e.g., Aspergillus terreus* produces itaconic acid during period 6–12 days after spore germination in pH below 2.3 which is suboptimum for mycelial growth; see extensive lists of literature on this subject in Thom and Raper (1945), Raper and Thom (1949), Foster (1949); development of sclerotia, hülle cells, etc. (Raper and Thom 1949, Lohwag 1941); development of conidiophores: method of production, nuclear condition, chromosome numbers; method of discharge or release of conidiospores; period of time over which fruiting can occur; numbers of spores produced; method of dissemination.

Formation of dicaryon (*Basidiomycetes*).—Relation of insects to initiation of sexual process (skip in case of formation of dicaryon prior to, during, or just after spore germination); anastomosis formation: fusion of compatible hyphae: in single spore cultures by manipulation, in nature by accident: is there a "guiding" substance secreted by one or the other hypha?; numbers of compatible strains per species, conditions of fusion in nature; pairing of nuclei and mixing of cytoplasm, diploidization of mycelium: homothallism and bipolar and tetrapolar heterothallism (Whitehouse 1949a, b, Brodie 1949, Fries, 1940), diploidization of both mycelia (Buller 1941a, b), diploidization in which only one mycelium is diploidized (Brodie, report to Mycological Society Sept. 1950): is donor or acceptor diploidized? fate of other mycelium?

Development of secondary (diploid, n + n, dicaryont) *mycelium*.—Nature of substratum, nutrients required (Lindeberg 1944, Nobles 1948), temperature, moisture, humidity, light conditions; development of rot in wood (Cartwright and Findlay 1947, Fahraeus 1949, Hilborn and Steinmetz 1943, Hungate 1940, Verrall 1945); production of enzymes (Zeller 1916, Foster 1949); relation to fire and sterilization of substrate (Moser 1949): fire: anthracobiont, anthracophilous, anthracoxenous, anthracophobous; sterilization of substratum: pyrophilous fungi: anthracobiont, anthracophilous fungi. Relation to neighboring organisms: rhizosphere bacteria and other fungi (Harley 1948) (assuming the hyphae of the mycelium to have a rhizosphere similar to that of the roots of vascular plants) (Katznelson *et al.* 1948), nearby fungi and other microoganisms: antibiotic and sympathetic effects (Robbins *et al.* 1945, Porter and Carter 1938, Weindling 1938, Wilkins 1949, Björkman 1949, Holtman 1947), inter-microorganism mycorhizal effects, if any (Höfler 1938, Friedrich 1937); nearby vascular root systems: antibiotic effects, mycorhizal formation: ectotrophic, ectendotrophic, endotrophic, peritrophic mycorhizae (Harley 1948, 1950, Hatch and Hatch 1933, Björkman 1949); production of decay in roots (Simmonds 1941); excess nitrogen production and utilization (Shantz and Piemeisel 1914); production of sclerotia and rhizomorphs (Lohwag 1941); area occupied by mycelium, rate of growth; bulk of fruit body in relation to amount of mycelium producing it; conditions of mycelium during freezing of substratum; are fruit bodies produced every year?; periodicity affected by: air and soil temperature, moisture, R-factor (R-factor is soil moisture value obtained by finding amount of water present in soil sample at time of collection expressed as a percentage times soil temperature value), effect of removal of fruit bodies on subsequent fruiting (Lambert 1938, 1941, Lange 1948).

Initiation of fruiting (Hein 1930).—Conditions of light, temperature, humidity, moisture (Buller 1909); number of initials initiated (Buller 1909); length of time lapsed between production of dicaryon and initiation of fruiting.

Development of fruit body (Hein 1930).—Conditions controlling which initial or initials develop; effect of insects, slugs and other mycophagists (Lambert 1938, 1941); conditions of development: soil or substrate conditions: temperature, humidity, moisture, R-factor; air conditions: light, temperature, humidity, moisture, evaporation stress, transpiration (Friedrich 1940); gravity (Buller 1909); source of water for rapid development of fruit body.

Maturity of fruit body.—Development of basidia and other structures of fructification (Lohwag 1941), completion of sexual process in basidium, meiosis, chromosome number, development of basidiospore sacklet and basidiospores (Lohwag 1941), discharge of basidiospores (Buller 1909–1950): conditions of temperature, moisture, humidity, light, gravity, air movement, evaporation, various gases in atmosphere; numbers of spores produced (Buller 1909), discharge and dispersion of basidiospores, period of time over which fruiting can occur, period of time over which spore discharge can occur.

Formation of dicaryon (Ascomycetes).—Initiation of ascogenous hypha, methods of hyphal fusion; period of time elapsed from time of spore germination; stages preceding: asexual spore production, pathogenic or saprobic development pattern.

Development of fruiting structure.—Tissue types: tissues arising from other than ascogenous cells; types of fruiting structures: within host tissues, external to host tissues; time lapse between formation of ascogenous hypha and formation of asci. Intermediate sporulation from asexual hyphae. (Arx (1949) showed how 13 genera of Fungi Imperfecti were involved in the life cycle of *Mycosphaerella tassiana* resulting in 63 synonyms including specimens from at least 132 host plants); development of asci; chromosome numbers; discharge of spores: influence of moisture, humidity, temperature, gravity; light (Flint 1942); numbers of spores produced.

5. Destruction of fruiting body.—By yeasts, bacteria, slime molds, molds, slugs, insects, other animals and man; certain species are especially desirable to animals as foods, many fruit bodies disintegrate after separation from desirable media.
6. Habitat (Friedrich 1936, 1937, 1940, Wilkins *et al.* 1937, 1938, 1939, 1940, 1946, Cooke 1948, 1950).—Habitat description: description of substratum: character of soil horizons especially those containing humus; soil-water relations: R-factor (Ubrizsy 1948, Feher 1933), pore space, frozen period; soil temperature at various levels where mycelium occurs; composition of organic matter used: cellulose, lignin, etc.; pH of soil; chemical analyses: K, Ca, P, N in its various combinations; other habitat factors (Cooke 1948, 1950): light intensity throughout season at point of initiation of fruit body development (Favre 1948, Wilkins *et al.* 1940, 1946); humidity: relative humidity of air, fuel-moisture stick determinations (Gisborne 1936, Cooke 1950), R-factor; air movement.
7. Communities.—Data for each habitat: composition of unions in each community; frequency in each community; dominance (volume or weight) in each community (Cooke 1950); if a fungus union is considered as a community distinct from the vascular plant community in which it occurs its aspect throughout the year must be considered (Cooke 1948, Favre 1948, Friedrich 1940, Lange 1948).
8. Biotic interrelationships.—*Response to other organisms:* mechanical disturbance of soil (Seaver 1935, Grainger 1946); soil antibiotics acting against fungi (Björkman 1949); burning (Moser 1949); mycophagy, animal or human: poisonous and edible species (Smith 1949), antibiotic effects, parasitism, allergy, effect of picking fruit bodies (Lambert 1941, Lange 1948); *effect on other organisms:* destruction of host tissues by wood rots (heart-rots, butt-rots, root-rots in forest trees), parasitic or pathogenic action; disintegration of litter by utilization as food; discoloration by chromogens (Davidson 1935, Verrall 1945).
9. Reactions to habitat as evidenced by fruit body production (Cooke 1948, 1950).—Gregariousness (response to habitat factor rather than genetic factors); average size of fruit bodies in various habitats and under various climatic conditions; reactions to climatic extremes such as frost, drought, freezing, dry air, etc.; reaction to fire or sterilization of substratum (Moser 1949); reaction to disturbance of habitat (Seaver 1935, Grainger 1946).
10. Phenology (general).—Times of maximum growth of mycelium; times of fruiting, including comparisons or contrasts between areas of differing climate, day length, etc.; period of spore discharge in evanescent as well as perennial fruit bodies; time of spore germination; period between spore germination and formation of dicaryon when compatible strains are developing in same area; period between formation of dicaryon and spore production; period between infection of host or substratum and fruit body development.
11. Parasites, diseases, etc., of fungi.—*Of mycelium:* in cases such as water molds where parasite is isolated with host, some species are fairly well known (Karling 1943, Couch 1945); for Penicillia parasitic on Aspergilli see Thom and Raper (1945); little is known about parasitism of mycelia growing within such natural substrata as logs, soil, heart-wood of trees, etc.; *of fruit bodies: casual mycophagy* by man, other mammals, slugs, insects, other fungivores: edible and poisonous species, secondary dietary supplements (Diehl 1939, Buller 1909); *obligate mycophagy* by animal parasites of fungus fruit bodies: certain protozoans and

Myxomycetes, fungus fleas, springtails, mites, sciarids, beetles (Scheerpeltz and Höfler 1948); *diseases of fungi: fungus diseases:* of fleshy, woody or other species; development of yeasts and bacteria on fleshy fruit bodies (Anderson and Skinner 1947); *bacterial diseases:* resulting from careless harvest of fruit bodies and penetration of mycelium by soil micro-organisms (Lambert 1941, Lange 1948).

12. Geographic distribution (Bisby 1943, Diehl 1937, Lind 1934).—Endemism, general abundance of the species, altitudinal limits (land and aerial) (Stakman and Christensen 1946).
13. History.—Fossil record (Andrews and Lenz 1947); effect of man on distribution: introduction to area (Large 1940, Hunt 1946, McCubbin 1946, Muskett 1950), spread after introduction (Leach 1935, Large 1940, Heald 1943), legal aspects of introduction (Fulling 1943, McCubbin 1946); epiphytotics or epidemics (Gäumann 1946, 1949).

Outline IV. Obligate Pathogens[6]

1. Basidiospore.—*Development and distribution:* Morphology, thinness of wall, relation to short life of spore; viability; method of discharge; numbers produced; method of dispersal; radius of effectivity from host to host. *Germination:* host tissues involved; conditions of humidity, moisture, temperature; period of time between alighting of spore and germination; development of germ tube, penetration of leaf. *Development of haploid mycelium:* development of mycelium in leaf; growth of mycelium through tissue at point of infection to tissue at point of optimum development of fungus; development of mycelium in tissue in area of optimum development: conditions mycelium encounters within host, path of mycelium through or between cells, development of haustoria, method of penetration of host cell wall by mycelium: chemical penetration (enzyme secretion), mechanical penetration; period of time during which this development occurs: conditions of external and internal environments.
2. Development of pycnia and diploidization.—Development under bark by monocaryon mycelium, bursting of bark by developing pycnium; pycnia with pycnospores become evident: development of receptive hypha, development of nectar-like secretion; relation of pycnospores and nectar-like secretion; initiation of protoaecia in relation to pycnia; attraction of insects to nectar-like secretion: composition of nectar-like secretion, species of insects attracted, means by which insects receive nectar-like secretion and included pycnospores; transportation of nectar-like substance with (+) or (−) pycnospores: reaction if second canker is of same strain, how long can cankers remain haploid?, reaction if second canker is of opposite strain: reception of pycnospore, fusion between receptive hypha and pycnospore: type of pore, method of fusion, function of nectar-like substance in this process. *Diploidization process:* rate of diploidization of canker cells; how rapidly does diploidization reach protoaecidium producing the aecidium; conditions in second, third and subsequent years after the first diploidization.
3. Development of aecidium and aecidiospores.—Lapse of time between diploidization and aecidium formation; *aecidium development:* cellular composition of aecidiospore chains, function of cells, type of aecidium developed, conditions at time of development of horns beyond host: humidity, temperature, moisture conditions of atmosphere and within host tissues; disintegration of aecidial horns; methods of aecidiospore discharge; methods of dispersion of aecidiospores; viability of aecidiospores, conditions causing death of aecidiospores: desiccation, heat, cold; how far can spores be carried: by ground winds, how high into upper air. *Germination of aecidiospores* and development of subsequent mycelium: place of germination: heteroecious and autoecious species; germination: age of invaded tissue; temperature, moisture, humidity of air; temperature, moisture of leaf surface; receptivity of host tissue; development of germ tube; penetration of germ tube into leaf tissue; local development of dicaryon hyphae: how extensive, type or types of haustoria produced.
4. Production and development of uredinium and uredospores.—Development of uredinium; development of uredospores: thickness of wall in relation to vitality, method of dispersal, resistance to adverse conditions: to what extent and to what conditions, for how long viable, conditions producing death. Germination of uredospores: host tissues (see above under aecidiospores), development of germ tube, conditions; local development of dicaryon mycelium in host tissues.
5. Production and development of teliospores.—In old uredinia or new telia;

[6] Based on the life history of *Cronartium ribicola,* the White Pine Blister Rust, as reported by Buller (1950). Certain aspects have been generalized to include other heteroecious rusts, and certain refinements can be made to include autoecious rusts and other obligate pathogens.

method of production of teliospores (hypobasidia); usually remain in position; method of germination or production of epibasidium (4-celled promycelium): conditions under which such germination takes place: atmospheric conditions, conditions within host; development of epibasidium: conditions of production of sterigmata, basidiospore sacklet, basidiospore—especially in respect to relative humidity of atmosphere surrounding teliosorus; conditions of violent discharge of basidiospores.

6. Phenology.—Time of development and discharge of basidiospores, of infection of host by basidiospores, of development of pycnium, of production and discharge of pycnospores, of development and discharge of aecidiospores, of development and discharge of uredospores, of development of teliospores and basidia.

Note: For a thorough discussion of materials suggested by the following headings see Gäumann (1946, 1949). The table of contents of the English edition (1949) could well be substituted for the headings chosen here.

7. Relative pathogenicity of the fungus.—Relations of weather (Foister 1935, 1946, Tapke 1948, Boughey 1949); conditions of physiology of host-parasite relations (Brown 1946); cytogenetic relationships (Johnson and Newton 1946); physiologic specialization (Reed 1935, 1946); restriction of fungi to host (Sprague 1944, Arthur 1934, Heald 1943). Control of fungi which cause disease (Roberts, 1936, 1946, Heald 1943). Conditions of host tissues at time of infection (Brown 1936): first alternate host: age of infected tissue, general health of tissue, general health of host organ and plant; second alternate host: age of tissues when infected, general health of host tissue, general health of host plant; both hosts: general environmental conditions: humidity, moisture, temperature, light conditions, conditions of soil relations, conditions of contaminating gasses in atmosphere. Conditions of host and affected host tissues during development of fungus mycelium: in tissues of both alternate hosts, development of conditions of immunity in the host (Ausemus 1943). Reaction of host tissue to fungus infection: Disease resistance (Wingard 1941), degree of normal activity of host tissue during course of infection, length of time required to inactivate host tissue, whether fungus kills tissue or relies on it for its own continued existence, possibility of infection eventually destroying host tissue; if host leaves are deciduous: how much earlier than normal do leaves fall, to what extent is efficiency in both organisms reduced.

8. Epidemiology (Gäumann 1946, 1949).—Conditions leading to epidemics, development of epidemics, decline of epidemics, effect of fungus on host at periphery of range of both hosts, effect of fungus on host at center of range of both hosts.

9. Geographic distribution.—In relation to first alternate host, in relation to second alternate host, rate of spread throughout present range, legislation to prevent spread and introduce control methods (Fulling 1943).

10. History.—See discussions of individual disease organisms in Buller (1950), Heald (1943) and Large (1940). By implication lists of synonymy in taxonomic treatments as Arthur (1934) give historical background.

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ACKNOWLEDGMENTS

The writer wishes to take this opportunity to thank the Ecological Life History Study Committee for the opportunity they presented to prepare this outline. R. F. Daubenmire, C. G. Shaw and D. B. Lawrence have read the manuscript and given valuable criticism, advice and suggestions.

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CULTURING PHYTOPLANKTON ON A LARGE SCALE

Several years ago it became increasingly evident that to carry on our research program the laboratory had to be provided with a large, dependable supply of plankton. Plankton was needed to feed clams, oysters and other mollusks, as well as their larvae.

Because of the scope and character of our work we often needed as much as 100 gallons of plankton per day. It was impractical and virtually impossible to grow such large quantities in glass flasks using the commonly accepted laboratory technique and employing culture media based on rigidly devised formulae, such as Miguel's. Fortunately, it was found that by adding some complete commercial fertilizers to sea water a rapid growth of phytoplankton could be induced and later maintained in heavy concentrations. Of the numerous fertilizing mixtures tried fertilizers 5–3–5 and 6–3–6, both used by tobacco growers, gave the best results (Loosanoff and Engle 1942). The formulae indicate the ratio of nitrogen, phosphorus and potassium. These fertilizers were mixed in a ratio of about one part fertilizer to one thousand parts water giving, as a rule, incomparably better results than those obtained with the standard chemical formulae prescribed for cultivation of plankton.

Using the fertilizers extremely rich cultures of Chlorella, Nitzschia, Prorocentrum, and many other plankton forms were grown on a mass scale at Milford Laboratory. A large, 3,000-gallon, oval tank was usually used as the container, but on several occasions the cultures were grown in the outdoor concrete tanks, each having a capacity of approximately 10,000 gallons. Obviously, because of the large quantities of plankton grown it is impossible to keep the cultures bacteria-free, or even single-specied. Nevertheless, it is comparatively easy to grow mass cultures composed of practically one species.

Our method of providing the laboratory with a dependable source of supply of large quantities of plankton worked very well in summer. However, with the onset of cold weather the culture in the outdoor tanks became poorer and eventually the tanks had to be emptied to avoid complete freezing. This was not especially inconvenient because at about the same time of the year the water in Milford Harbor, which was pumped in to supply the laboratory needs, became so cold that the mollusks began to hibernate, and could not be used in experimental work until the increase in temperature the next spring.

The situation was radically changed when Milford Laboratory was provided with warm running sea water during the cold season (Loosanoff 1949). Because of this innovation it became possible to conduct throughout late fall, winter and spring many experiments which formerly had to be confined to the summer period only. The opportunity was especially widely utilized in conditioning to ripeness oysters, quahogs, soft clams, mussels, and other bivalves, from which normal spawn could be obtained when needed for the experiments (Loosanoff and Davis 1950).

The initiation of extensive winter activities again presented the problem of having on hand a sufficient supply of plankton food. Naturally, it was impossible to grow the culture in the open tank outside because it would freeze on

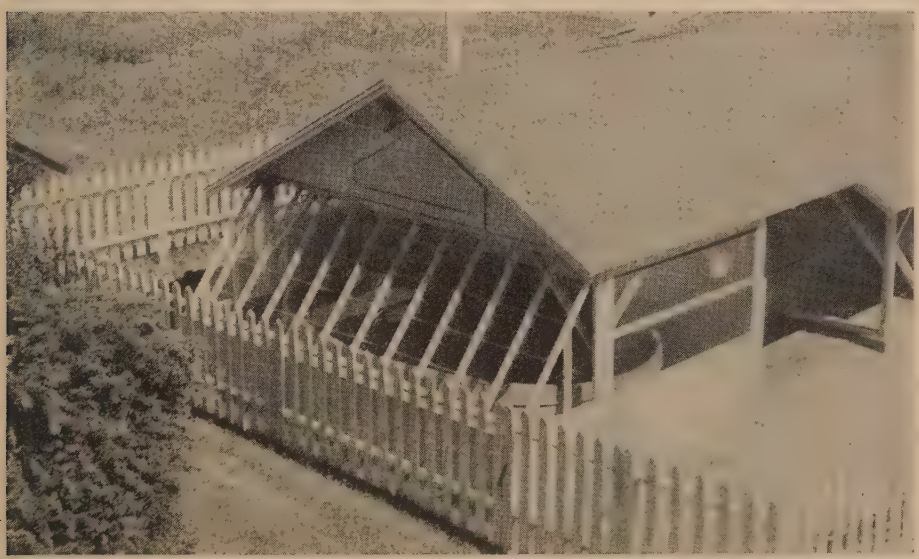

Fig. 1. Glass enclosure of plankton greenhouse. U. S. Shellfish Laboratory, Milford, Connecticut.

cold days. The problem was solved by designing and constructing a special enclosure resembling in its main features a regular greenhouse used for cultivation of plants in winter (Fig. 1). A shallow wooden tank of approximately 3,000-gallon capacity occupied the center of the enclosure, the walls of which were made of special greenhouse glass that permitted penetration of the ultra-violet rays needed for growth of phytoplankton. To maintain the culture at the desired temperature an automatic oil stove was installed in the house. Using this stove it was possible to keep the temperature of the culture at about 15.0° C. even on the coldest days of the winter. To provide the additional light needed during the period of the year when the days are short and the amount of light limited, a large fluorescent light fixture was suspended over the culture tank.

Because carrying buckets of culture from the plankton greenhouse to the main laboratory building is laborious and inconvenient, a provision is made to pump the culture directly from the tank to a central basin in the laboratory. From it the plankton is distributed by gravity, through a system of hoses and pipes, to various reservoirs from which it is slowly added at the desired rates to the flowing sea water.

When some of the culture from the tank is used the loss in volume is compensated by pumping in the same quantity of new sea water. From time to time some fertilizer is added to the culture. It was found that by using our method it is possible to remove daily from the tank about 1/20 of its volume and, yet, to allow the plankton population to remain at the same level or even to show a steady increase.

Under the conditions described the culture has been doing very well for the past several years. Its density is regularly determined by using a Fuchs-Rosenthal counting chamber, commonly used for counting erythrocytes and leucocytes. The density is easily maintained between 25 and 30 million cells per cc. of *Chlorella sp.* and on some occasions a population of approximately 45 million cells per cc. was reached. In general, the culture requires very little care. Once started it may be maintained a long time without emptying and washing the tank. Once the same culture was carried on for about 18 months and was still good at the end of this period, maintaining a population of approximately 35 million cells of Chlorella per cc.

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A REMNANT OF OLD WHITE PINE-HEMLOCK FOREST IN NEW HAMPSHIRE

Most of the "old growth" stands of white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) in New Hampshire were destroyed in the 1938 hurricane. Recently a very small strip containing trees 150–200 years old was discovered near the village of Bradford in southwestern New Hampshire. It occupies about 2 acres on a sand bar bordering the Warner River at an elevation of 680 feet. The stand (Fig. 1) contains 20 white pines, many of large size, and a larger number of hemlocks and hardwoods. Hurricane damage occurred on the edges of the stand, and one large pine was cut at about that time. One pine was also felled by the great storm of November 25, 1950. On a square one-quarter acre plot relatively little disturbance has occurred, and this was selected for detailed study.

On a per-acre basis there were 360 trees 2″ in diameter and over, 64 of which were white pine, all over 14″. Hemlock and beech (*Fagus grandifolia*) composed the bulk of the other trees with northern red oak (*Quercus rubra* var. *borealis*), yellow birch (*Betula lutea*) and red maple (*Acer rubrum*) also represented among the larger trees. White pine also composed one-half of the total basal area of 643 sq. ft. and over 60% of the volume, estimated at 115,000 bd. ft. per acre. The largest pine measured 49.4″ in diameter at breast height and 61″ at stump height. This tree stood about 150 ft. from the group included in the plot. Height was determined by hypsometer to be 130 ft. When viewed from an adjoining elevation, there appeared to be no difference in the heights of the large pines. They are certainly all in excess of

FIG. 1. Interior view of stand showing predominance of beech and hemlock in the understory.

100 ft. The one large pine cut about 12 years ago left a stump 52″ in diameter. Ring counts along several radii averaged 153 years. A 26″ hemlock stump gave a count of 140 years.

It seems reasonable to conclude that the largest trees are 100 to 150 years of age and that none exceeds 200 years. Increment borings taken on several large pines and hemlocks indicated growth during the past 10 years to have averaged about 1″ in diameter and 5″ during the past 50 years. Height growth appeared to have ceased entirely. The living sapwood consists of a cylinder only one to two inches thick. The heartwood has the characteristic salmon-pink color that gave the name "pumpkin pine" to old growth timber. The bases of the trees (Fig. 2) terminate in prominent buttresses leading to the main roots, characteristic of trees growing in flood plains.

The stand occupies a narrow sand bar beside the river. The soil can be classed as very fine alluvial sand. Moisture is abundant, the water table being only 2 to 3 feet from the surface. Drainage is good except for short periods in spring when the water level must reach the tree roots. Decomposition is rapid for an old coniferous stand. The litter is about one inch in thickness and consists of pine and hemlock needles, cones, twigs and hardwood leaves. Below this is a humus layer 3 inches thick similar to fibrous mor in character. Below this is a one-half to one inch dark brown, peaty layer. The leached horizon is well-developed and in some places over 2″ thick. The brown B-layer is relatively thin, rarely exceeding 3″ followed by the unaltered sand.

The subordinate vegetation is varied and rich, and includes species that have invaded from former pastures and cutover land nearby. The following were listed with no attempt to determine relative abundance, frequency, nor propor-

FIG. 2. Basal portion of large white pines showing buttressed roots.

tion of the area occupied: (Nomenclature follows eighth ed. of Gray's manual by M. L. Fernald, 1950).

Shrub Layer

Ground hemlock (*Taxus canadensis*)
Witch hobble (*Viburnum alnifolium*)
Witch hazel (*Hamamelis virginiana*)
Beaked hazelnut (*Corylus rostrata*)
Blackberry (*Rubus* sp.)

Tree Reproduction

Beech *Fagus grandifolia*
Hemlock *Tsuga canadensis*
White Pine *Pinus strobus*
Yellow Birch *Betula lutea*
Northern Red Oak *Quercus rubra* var. *borealis*
White Ash *Fraxinus americana*
Black Cherry *Prunus serotina*
Red Maple *Acer rubrum*
Sugar Maple *A. saccharum*
Striped Maple *A. pennsylvanicum*
Hop Hornbeam *Ostrya virginiana*

Ground Vegetation

Typical coniferous forest species

Wintergreen *Gaultheria procumbens*
Arbutus *Epigaea repens*
Partridge berry *Mitchella repens*
Canada mayflower *Maianthemum canadense*
Wild sassaparilla *Aralia nudicaulus*
Indian cucumber root *Medeola virginiana*
Twisted stalk *Streptopus amplexifolius*
New England Aster *Aster acuminatus*
Red trillium *Trillium erectum*
Beech drops *Epifagus virginiana*
Indian pipe *Monotropa uniflora*

Meadow species

Royal fern *Osmunda regalis*
Cinnamon fern *Osmunda cinnamomea*
Lady fern *Athyrium filix-femina*
New York fern *Dryopteris novaboracense*
Goldenrod *Solidago* sp.
Loosestrife *Lythrum* sp.
Meadowrue *Thalictrum dioicum*
Poverty grass *Danthonia* sp.

Lutz (1930 b) reported the composition of the remnant of original white pine forest at Heart's Content, Pennsylvania, as beech, hemlock, maple, birch, white pine and chestnut, which agrees well with the composition reported here. He listed a much larger number of tree species, indicative of the more Alleghenian region. Probably, if the Bradford stand were of equal size many other species would be recorded. In another paper (Lutz 1930a) he listed all the coniferous forest ground vegetation recorded here and a host of other species. Among the shrub layer, however, *Taxus canadensis* and *Corylus rostrata* were not included. Lutz's conclusion that the high white pine representation in the hemlock beech association is a temporary condition is confirmed by the prevalence of hemlock seedlings and saplings in the Bradford stand, and the complete lack of white pine reproduction over 6″ in height.

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SEASONAL PATTERNS OF OYSTER SETTING IN THE JAMES RIVER AND CHESAPEAKE BAY[1]

The James River seedbeds are one of the few oyster-growing areas of the world still operated successfully as a free fishery on natural oyster grounds. It is characteristic of free fisheries that much is taken out and little is put back. For some 50 years, the James River seedbeds have continuously furnished most of the seed-oysters (young oysters) for the planters of Virginia. That they are still productive is strong testimony to the natural fitness of the area for oyster culture. Yet, their survival as seed grounds must be attributed in no small measure to the laws prohibiting modern mechanized harvesting methods.

The James River seed area is comprised of public oystering grounds, the boundaries of which were established by the Baylor Survey of 1894. The area extends from near the James River Bridge at Brown Shoal to Deep Water Shoal Lighthouse (Fig. 1). Its importance as a source of seed-oysters for the entire oyster industry of Virginia, places it high on the list of fishery problems for biological study. Failure of the seedbeds would be catastrophic for the industry, planters and tongers alike; improvement,

[1] Contributions from the Virginia Fisheries Laboratory, No. 34.

FIG. 1. Map of Lower Chesapeake Bay showing major tributaries and sampling stations.

which seems quite possible, would add to the nation's food supply and enhance the natural resources of the state.

The most important and basic biological feature of the James River seed area is the excellent strike (spatfall) which occurs each year without fail. Several years ago the Virginia Fisheries Laboratory began a study of oyster setting in the James River. The immediate problem was to determine whether planting shells in late summer would increase the setting and survival of spat, for it had been observed that sets occurred rather frequently during August and September. In this paper results are presented from only one type of data, the weekly setting records. The seasonal pattern of setting is compared with other areas and possible explanations are discussed.

METHODS USED IN TESTING WEEKLY SPATFALL

Test shells were placed in bags of one and one-half inch chicken wire. These bags were 18 inches long and 8 to 10 inches in diameter and so constructed that when filled all shells were less than four inches from the outside. Twenty shells were marked and distributed randomly in each quarter bushel bag for counting. The bags were then placed on the river bottom in pairs and left for one week. After exposure, the inner faces of the marked shells were examined for oyster spat. Successive series of bags were

TABLE I. *Variations in setting at Wreck Shoal, James River*

Year	Length of setting season in days	Average number of spat per shell face	
		Total of all weekly sets[2]	Greatest weekly set
1947	85	157	35.0
1948	98	85	18.2
1949	99	108	18.9
1950	84	109	39.2

[2] The average number of spat which would have set on one shell face during the season if that shell face were cleaned and returned to the water once a week. In practice a new bag of clean shells was exposed each week and all the weekly counts were added to get a total for the season.

placed on representative bars throughout the setting season. Stations were located on three oyster bars: Brown Shoal, just below the seed area; Wreck Shoal, lying in the center of the seed area among the most important bars in the river; and Deep Water Shoal, the last commercially important bar at the upper end of the seed area.

RESULTS

Weekly samples from Wreck Shoal for the summers 1947–1950, inclusive, show:

1. That setting is continuous for about three months each year, from the first of July to the first of October (Table I).
2. That the rate of setting is fairly consistent from year to year with a peak set of 18 to 39 spat per shell face per week. There have been no failures and the setting has been distributed over several weeks with the total and greatest weekly sets being of similar magnitude each year.
3. That the most intense sets occur in late August or early September and that July sets are relatively unimportant.

In Figure 2 the setting data for Wreck Shoal are expressed as weekly and monthly percentages of the total season's set. This permits comparison of seasonal distribution of set for different seasons and different bars regardless of the magnitude of the set. The four-year average was obtained for comparison with other bars and rivers. This graph shows that the July set was never more than 10 per cent of the total set during the four-year period, and that the peak of setting usually occurred near the end of August or the first of September.

In any particular year the seasonal distribution of setting on other bars in the James River corresponds closely with that of Wreck Shoal (cf. Fig. 2 and Table II). The average for these bars is very similar to the four-year average for Wreck Shoal. Thus Wreck Shoal may be considered typical for the James River as far as the pattern of setting is concerned. Loosanoff (1932) found a similar pattern at Mile's Watchhouse in 1931.

The James is compared with other Virginia rivers in Figure 3. Yorktown Fish Pier and Pages Rock are in the York River, while Island Bar is in the Corrotoman River, a branch of the Rappahannock. An early set of considerable importance occurred in these rivers in addition to the late set typical of the James. In 1950, 88 per cent of the set at Island Bar occurred in July. Although weekly setting records for the Rappahannock River are lacking, other records indicate that the 1948 pattern in the Corrotoman is fairly typical.

In Table III, figures on the distribution of setting show that early setting is of major importance in Maryland waters, again in contrast to the late set in the James River. St. Marys River and Holland Straits exhibit this pattern very clearly, but setting is so extremely light and spasmodic on Parker Moore Bar that the average figures may not be reliable.

It has been shown that only a small part of the strike in the James River occurs in July, while in other tributaries of Chesapeake Bay a large or major portion of setting takes place

TABLE II. *Seasonal distribution of spatfall, James River (Percentage of total set occurring monthly)*

Month	Nansemond Ridge	Brown Shoal		Mile's Watchhouse[3]	Deep Water Shoal			Average	Wreck Shoal Four Year Average
	1947	1949	1950	1931	1947	1949	1950		
June	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.1	0.0
July	3.8	9.9	4.9	10.6	4.6	2.1	1.8	5.4	7.0
August	64.5	71.5	18.3	21.4	58.7	79.8	38.9	50.4	48.9
September	31.7	18.6	76.2	65.5	36.7	18.1	59.2	43.7	43.7
October	0.0	0.0	0.6	1.9	0.0	0.0	0.0	0.4	0.4

[3] Data from Loosanoff 1932.

during this month; and, late sets may be expected in many tributaries of Chesapeake Bay, but they are of major importance in the James River. Thus, the setting pattern of the James River differs from that of other areas in Chesapeake Bay and on the Atlantic Coast of North America (Beaven 1950; Hopkins 1931; Loosanoff and Nomejko 1951).

Discussion

The question may be asked, "What is the mechanism or combination of factors that causes late setting in the James River?" Numerous combinations of chemico-physical and biological factors may be responsible for variations in setting (Loosanoff 1949). The discussion that follows will be limited to certain biological

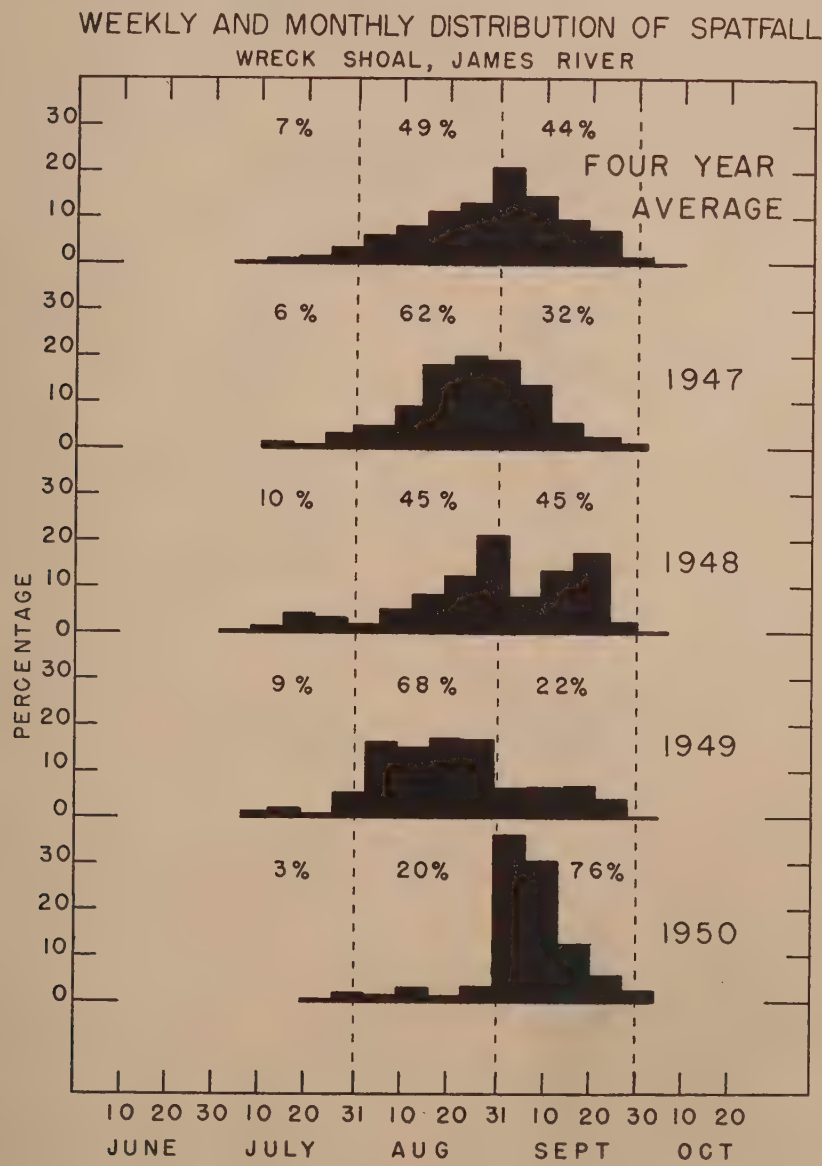

Fig. 2. Weekly and monthly distribution of spatfall, Wreck Shoal, James River.

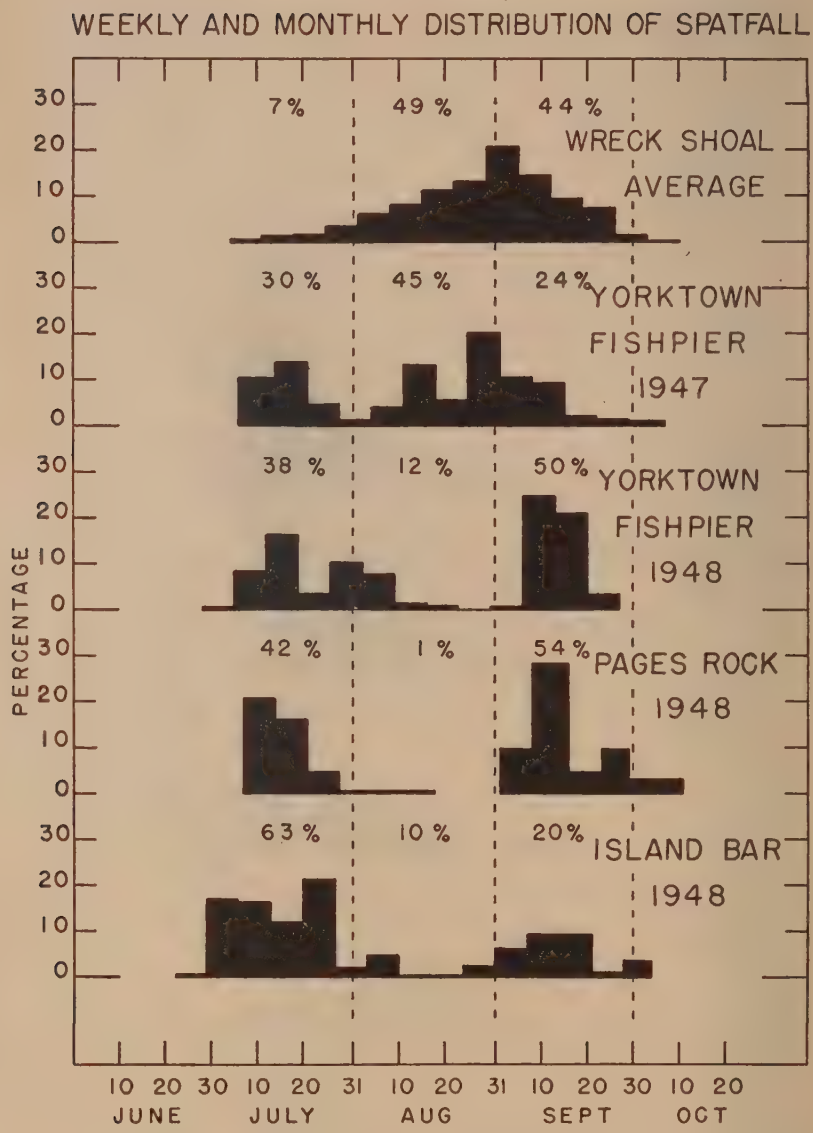

FIG. 3. Weekly and monthly distribution of spatfall at several Virginia localities.

characteristics wherein the James River seems to differ from other oyster-growing areas in Chesapeake Bay.

Small size of brood oysters

The use of the James River as a seed area and the slow growth of oysters there preclude the development of any extensive stock of large brood oysters. No important deep water beds which are out of reach of tongers have been located, so nearly all beds are subject to tonging each year. The remaining oysters are predominantly two-year old, one-year old, or current-year spat. Since growth is very slow in the seed area, these oysters are all small. Two-year old oysters are one to two inches in length depending upon the location. While these may make up a considerable part of the total volume of oysters, the yearlings and current-year spat are far more numerous.

TABLE III. *Seasonal distribution of spatfall in Maryland waters*[4]
(Percentage of total set occurring monthly)

Month	St. Marys River Seminary Bar	Holland Straits Cinder Hill Bar	Chesapeake Bay Parker Moore Bar
	1945–1950 average	1949–1950 average	1944–1950 average
June	17.9	7.5	13.2
July	77.3	66.9	28.7
August	4.8	23.2	25.2
September	0.0	2.2	25.2
October	0.0	0.2	7.8

[4] Mr. G. Francis Beaven of Chesapeake Biological Laboratory has kindly furnished the data in this table.

It is possible that oysters in the lower James and Hampton Roads furnish spawn which is carried into the seed area by tidal currents; but if we assume that setting results from spawn produced within the seed area, then the brood stock consists of large numbers of small oysters each of which produces a very limited amount of spawn. Thus small size and large numbers of oysters, and their associated spawning characteristics may constitute a significant difference in the oyster ecology of the James River as compared with other areas in Chesapeake Bay, with the possible exception of St. Marys River.

Scarcity of plankton

The paucity of net plankton in the James is another feature of interest. While detailed counts are not available, observations on three years plankton samples (No. 20 net), suggest that fewer species and smaller numbers of individuals occur in the James than in other rivers in Tidewater Virginia. A scarcity of net plankton does not necessarily imply a scarcity of nannoplankton or of oyster food. Furthermore, there is no evidence that the ultraplankton believed necessary for larval survival is lacking in the James. Conflicting views on the sizes and kinds of organisms utilized by oysters as food are given in the current literature (Korringa 1949). A paucity of net plankton could result from feeding activities of some population such as oysters at a lower level of the food chain.

The belief that plankton is scarce is supported by the observation that oysters are usually in poor condition in the James. Since these oysters fail to accumulate much glycogen in the fall, it is reasonable to assume that their spawning might be delayed by the continued feeding in spring and summer necessary to acquire the essential food reserves. Furthermore, the development of oysters to maturity or first spawning, assuming that size is more important than age, may be delayed by poor food conditions. It is possible that food scarcity causes a stock of oysters to spawn late through delayed maturity and poor condition.

Sex ratio and protandry

Coe (1938) reports among first spawners in New England as few as eight females per hundred males when nutritive conditions are not favorable. In Delaware Bay and at Beaufort, N. C., the female ratio averaged over forty per hundred but no collections from Chesapeake Bay are mentioned. The James River brood stock undoubtedly includes a high proportion of first spawners each year and it is quite apparent they are not living under favorable growing conditions. Coe (1938) and Needler (1932) also show that as a result of sex reversal the female ratio becomes higher as the population grows older and that eventually females may exceed males. Further study is needed to determine the roles of protandry and sex reversal in the failure of early sets and the success of late sets.

The James River appears to be exceptionally consistent from year to year in the amount and seasonal distribution of oyster sets. This may indicate that fewer factors regulate or limit the sets in the James than elsewhere but this very consistency may increase the difficulty of defining and delimiting those factors.

SUMMARY

1. A study of seasonal patterns of oyster setting in the James River, Virginia, shows that setting is usually continuous for about 90 days, from the first of July to the first of October.

2. Setting is consistent from year to year, no failures having occurred during this study.

3. Setting is typically late in the James River with over 90 per cent occurring after the first of August in contrast to other areas of Chesapeake Bay which often get a major part of their spatfall in July.

4. The peak of setting occurs around the first of September.

5. In any particular year the rates of setting may vary from bar to bar but the percentage distribution of setting over the season is similar for all bars.

6. The small size of brood oysters, the scarcity of net plankton, and sex ratio and protandry are suggested as possible contributing factors to the late set in the James River.

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RANGE AND HABITAT OF THE CLAM *POLYMESODA CAROLINIANA* (BOSC) IN VIRGINIA (FAMILY CYCLADIDAE) [1]

The clam *Polymesoda caroliniana* (Bosc), which ranges north and eastward in brackish waters from Lavaca Bay, Texas,[2] has not previously been reported north of the Neuse River, N. C. (Van der Schalie 1933). On 7 April 1947, Richard Hoffman found several shells on the beach above Swann Point on the James River, a tributary of Chesapeake Bay (Fig. 1). On 20 April 1947, J. P. E. Morrison (personal communication) and Hoffman found living specimens in the mud and detritus around the knees of cypress trees one-half mile above Swann Point. These records are included in this paper through the courtesy of Dr. Morrison of the U. S. National Museum.

In the spring of 1949, the authors made several field trips to determine the distribution and habitat of the species in Tidewater Virginia. Figure 1 shows the areas visited and the places where *Polymesoda* was found. On the north bank of the James, clams have been found from slightly above Jamestown Island to the lower end of Mulberry Island, a distance of 17 nautical miles by river. The salinity range in this area varies from nearly fresh water at Jamestown to about 15 parts per thousand at river stations opposite the tip of Mulberry Island. Table I gives the number, average length, and range in length of clams collected at each station. All clams in each collection were measured. These collections are deposited at the U. S. National Museum.

[1] Contributions from the Virginia Fisheries Laboratory, No. 35.

[2] Dr. J. P. E. Morrison states that the specimens in the United States National Museum from Vera Cruz and Tampico, Mexico, belong to the closely related species *P. triangula* (Von dem Busch) (personal communication).

Polymesoda has not been found in the York River but several potential habitats remain to be examined.

Description of Habitats

Polymesoda is apparently restricted to intertidal habitats in the James River. Most clams have been found in a strip between mean low tide and one foot above this level. A careful search has failed to reveal the presence of this species either below the low water line or on oyster bars in the vicinity of known habitats.

These brackish-water clams have been found in three apparently diverse habitats:

1. Open river shores with eroding, sedge-matted banks. Polymesoda were found in small protected crevices and often in the bottom of small depressions partially filled with finely divided plant debris and black mud. The clams were in depressions at a level six inches below the bases of living plants (*Panicum* and *Juncus*) but usually imbedded in a substratum well matted by the roots of dead plants. Stations (see Fig. 1): Mouth of Back River at Jamestown (4); Treasure Island (5); Mouth of Skiffes Creek (7); Lower Mulberry Island (10).

2. Under thick algal carpets on muddy banks of tidal creeks. Clams were found under small bulges in a thick cohesive carpet of algae covering muddy flats. This was a most remarkable habitat, for the algal mat was one-quarter to one-fifth of an inch thick and probably had resulted from several seasons' growth. This implies that the larvae or young clams penetrated the mat and flourished under it, for clams of greatly varying sizes were found here. Small clams were abundant only in this habitat. The soil under the algal blanket was a fine black

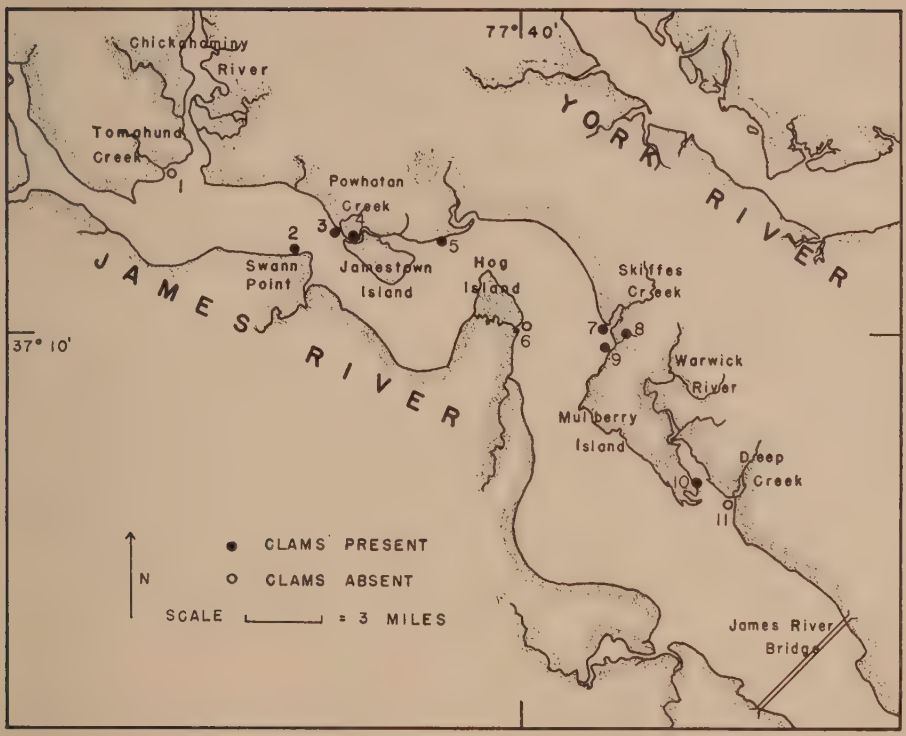

FIG. 1. Map of James River showing collecting stations.

silt with a distinct marsh odor. An accumulation of trash on the creek and the proximity of warehouses suggested polution. Stations: Creek at Ft. Eustis (8).

3. In crevices of riprap beach. Clams were found wedged between and under rocks and only slightly imbedded in the sparse soil. The species was more abundant here than at any other habitat examined; half a dozen clams could be found in an area two feet square. It was fairly obvious that these clams had set and grown in the rock crevices, for the beach below was loose sand and there was no evidence that they had washed in from elsewhere in the vicinity. Stations: Riprap beach at upper end of Mulberry Island (9).

TABLE I. *Collections of* Polymesoda *in Virginia*

Place	Station number	Date	Number of clams collected	Mean length (mm.)	Length range (mm.)
Swann Point (Hoffman)	2	7 Apr. 1947	6 valves	—	—
Swann Point (Morrison)	2	20 Apr. 1947	many	—	—
Powhatan Creek	3	5 Apr. 1949	shells only	—	—
Treasure Island	5	3 Mar. 1949	10	36	27–46
Treasure Island	5	12 Mar. 1949	17	28	12–37
Back Creek	4	12 Mar. 1949	15	31	14–44
Skiffes Creek Area	8, 9	7 May 1949	38	30	11–48
Skiffes Creek Area	8	25 May 1949	32	33	14–42
Skiffes Creek Area	7	25 May 1949	10	35	32–39
Skiffes Creek Area	9	25 May 1949	30	31	15–49
Lower Mulberry Island	10	25 May 1949	7	32	22–43
All samples			159	31	11–49

Discussion

While these habitats are superficially quite different, they have at least two common characteristics:

(a) all offer protection from the mechanical action of tides and currents
(b) all are intertidal and are exposed to the air at most low tides.

Conditions of low oxygen in the substratum do not seem to offer any barriers to *Polymesoda*. Clams were kept several months without dying in small bowls with little change of water and often with the substratum nearly dry. They are well called marsh clams, although, as indicated by Van der Schalie, the species will live for some time in sea water. Their ability to maintain a position in the substratum seems definitely limited despite a well-developed foot. The most essential requirement of the habitat seems to be a moderate amount of protection from the action of waves.

There is no reason to suspect that *Polymesoda* has been introduced into the James River in recent years. Its absence from previous lists reflects the general lack of faunal information in Virginia particularly in brackish waters. *Polymesoda* is limited to slightly brackish waters and the family is a brackish to freshwater transition group. The species now has a discontinuous distribution and extension of its range appears to be precluded by salt and freshwater barriers. Because the habitats are very limited in area, a local population, such as occurs in the James River, is relatively small in total numbers. This population has probably been isolated from those of other river systems to the south since sometime in the Pleistocene. If this is true the species is interesting from the genetic and evolutionary standpoint.

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A GROUND PLAN FOR A BIOLOGICAL RESEARCH PLANT

Thirty-five years ago the writer undertook to control temperature, atmospheric moisture, evaporation, air movement, and so far as possible, light, in a large series of experiments. The biological material was an hemipterous insect which feeds on plants. Constant and variable conditions were used, the latter simulating average days, and supplemented with out-of-door checks and observations.

The glass-roofed room used for this work was attached to the east end of an ordinary building which cast shadows over the air conditioned experimental units beginning soon after 1:00 P. M. for some of them and later for others. Some of the units fell into full shadow in the early afternoon, others later. Due to the varying position of the sun and the necessity of arrangement of the units, this could not be avoided. The shadows interfered with all controls and gave unequal effects on the food plants living under reduced light due to several thicknesses of glass. The arrangement of glass-roofed space with reference to use in experiments with animals has evidently been an outgrowth of the idea that too much sunlight is usually available and that it may be reduced by haphazard shadows with no ill effects. Most institutions have haphazard arrangements resulting from architectural plans. A scientific approach calls for symmetrical and uniform sun and sky exposure. Otherwise the investigator cannot control light and other sun and sky radiations without shutting them off altogether. This unfortunately renders the control of other factors easier. Symmetrical lighting and known periods of sun exposure become scientifically essential the moment long exposure to weak ultraviolet light has been demonstrated to act as a reproductive stimulus (Sabrosky, Larson, and Nabours 1933; Marshall and Bowden 1934; Bailey 1950), or to be important in the control of populations (Shelford 1951). Some recent investigations have stressed duration of sunshine in connection with bovine reproduction (Mercier and Salisbury 1947). Radiation control for plants and photoperiodism for birds and plants need no comment.

As an outgrowth of his experiences, the writer has drawn a rough outline of a plan for a biological plant in which some of the neglected factors can be controlled (Fig. 1). This is based on location on a nearly level plane at 40° N. Latitude. The objective is to provide space for glass-roofed houses, outside areas for kennels and cages, gardens, and ponds, including an area of 200 ft. sq. (a little less than 40,000 sq. ft.) which will receive all the hours of sunlight which are available above the tops of trees and buildings 70 ft. high. A larger space not

symmetrically lighted is also provided. There must be a distance of 235 to 240 ft. from the sides of the 200 ft. sq. area to the nearest 70 ft. structure. As will be noted, the building and grounds will cover an ordinary city block approximately 600 ft. square. The area to the south may be surrounded by: (a) glass-roofed buildings for plants and animals, for instruction, and use in some of the less technical operations; and (b) an opaque-roofed building for dark rooms, animal houses, and equipment storage.

It will be noted that the proposed main building must have its south side adjusted to the angle at which the sun comes above the obstructing trees and buildings on June 21. The wings must be arranged so that the building will not cast shadows at any time on most of the 200 ft. sq. area. This arrangement is not intended to imply anything as to the interior of the main building or smaller buildings.

To consider the facilities of the plant, one by one, we note that: (a) glass-roofed houses in full available sunlight may have the roof treated or interior portions air conditioned under uniform sun and sky lighting. Ordinary glass houses at the sides of the yard will be better as to sun and sky exposure than most university greenhouses because they will come into sun or shade throughout their entire length within a very short period; (b) out-of-door garden, pen, and cage space is important to both botanists and zoologists and all other biologists. For example, on the animal side, to test the effect of ultraviolet light and moisture on quail, the animals must be caged outside and the experimental group exposed to a small excess of ultraviolet for a month or more (Shelford 1951). At the present time four men of the permanent staff of the Department of Zoology of the University of Illinois and their graduate students are using out-of-door cage, kennel and garden space (30,000 sq. ft.; ponds, 15,000 sq. ft.) adjacent to very badly arranged buildings. In considering garden space, some is widely used by botanists. At the University of Chicago 35,000 sq. ft. are in use within 1,000 ft. of the main building. Ponds are essential for studies of fishes, in parasitology, in ecology, and studies of aquatic plants. Without out-of-door experiments and checks, applications of experimental results to practical problems are delayed, and misleading conclusions may be drawn.

As to possible sunshine, Table I and Figure 1 bring out the following important points. A comparison of the total possible sunshine on the well-lighted area with the total possible on a level plain, shows that a 70 ft. wall around the area placed as indicated shortens the possible

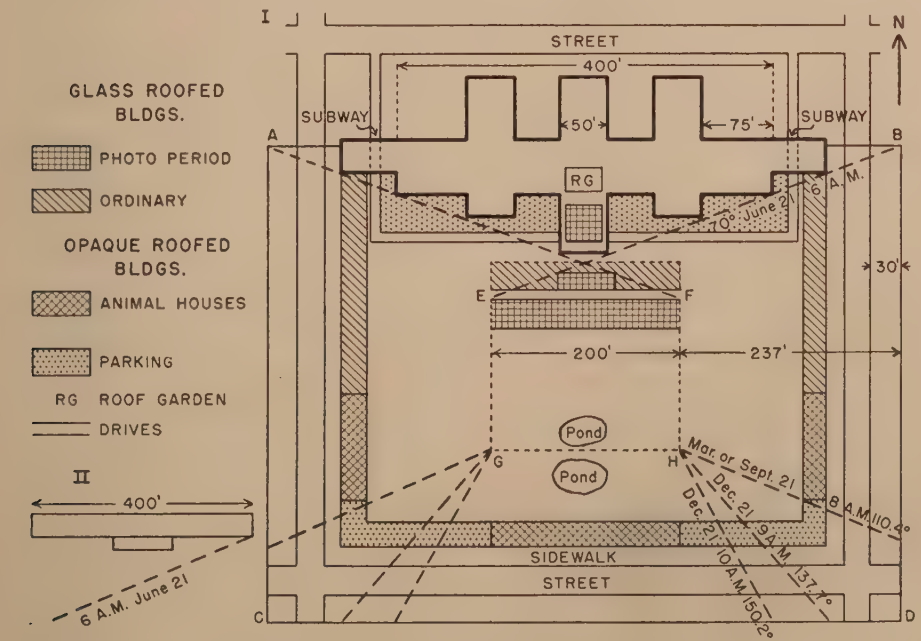

FIG. 1. Proposed ground plan for a biological research laboratory that permits symmetrical and uniform exposure to sun and sky.

TABLE I

Sunshine and ultraviolet conditions. Column 3 shows the length of the period of possible sunshine at 40° N. Latitude from March 22 to June 21, and roughly June 22 to September 21 on a 200 ft. sq. plot south of a building designed to fit the June 21 azimuth at 6:00 A.M. (surrounded by a 70 ft. wall of buildings) as shown in Figure 1.

The total possible hours of sunshine are omitted but can be approximated within 2% by adding 3 hours, 33 minutes to the figures in column 3. Column 4 shows the hours of sunshine against the center of the south wall of a building 400 ft. long as shown in Figure 1 (II, lower left). Note reversal on May 1 and August 15. Column 5 shows the smoothed average ultraviolet energy accumulation in Luckiesh's (1946) E-viton hours per cm² at Cleveland, Ohio, for 1935 and 1936. Column 6 shows the mean monthly accumulation of milliwatt minutes per cm² at Washington, D. C., 1941 through 1944, April, May, June, standing opposite the 7th of the respective months in column 1 and for July, August, and September standing opposite the 1st of the respective months in column 2 and slightly to the right (after Coblentz 1945).

1	2	3 Azimuth	4 Flush	5 E-v. hr.	6 M. watt. min.
Mar. 22	(Sept. 21)	9 20−	9 20−	91	
Apr. 1	Sept. 15	9 20+	9 20+	95	
Apr. 7	Sept. 7	9 30	9 30	108	690
Apr. 15	Sept. 1	9 40	9 40	106	720
Apr. 22	Aug. 22	9 50	9 50	111	
May 1	Aug. 15	10 20	9 10	120	
May 7	Aug. 7	10 30	8 50	135	1015
May 15	Aug. 1	10 40	8 30	150	1020
May 22	July 22	10 50	8 10	160	
June 1	July 15	11 10−	7 50	174	
June 7	July 7	11 10+	7 50−	173	1127
June 15	July 1	11 30−	7 50−	167	1109
(June 21)	June 22	11 30+	7 50	167	

sunshine period by 3 hours, 20 minutes to 3 hours, 45 minutes. The length of the period in such an area can be calculated for any latitude and is the same throughout the well-lighted area, except for breaks in the 70 ft. surrounding wall of buildings and trees. Since the angle of the sun over the wall is known, the investigator can easily correct breaks in the surrounding wall with screens of his own. Seventy feet is arbitrary; the height of the surrounding structures must be known and used in the calculations for each locality.

One striking feature brought out by Table I is the effect of a building 400 ft. long on the period of possible sunshine on a point in the center of its south side (II, at lower left of Fig. 1). This effect is shown in Column 4 of Table I. For the first 30 days after March 22 the total possible hours of sunshine are the same for the entire area south of a building 400 ft. long on an east-west line and without the 70 ft. wall and south wings of Fig. 1 (I). Beginning about May 1 at the center of the south wall, the possible hours of sunshine decrease until June 21 and then increase again until August 22. The maximum difference from the sunshine period inside the 200 ft. sq. area is 3 hours, 42 minutes. This tendency holds good throughout the triangle south of the main bulding (I) marked by the two 70° lines indicating the sun's position and must be calculated for each point in the triangle. In spite of this, a common location for green houses is all or in part within such a triangular area. The fact that intensity and duration of some wave lengths are important, makes all facts bearing on errors in exposure significant.

Column 5 of Table I shows the weekly ultraviolet intensity on the roof of the Nela Park (Cleveland, Ohio) General Electric Laboratory in 1935 and 1936 (from Luckiesh 1946). It is a smoothed curve of mean weekly sums of E-viton hours during the increase from March 22 to June 21 and from September 21 back to June 22. The curves were plotted separately but being comparable but irregular, the mean was taken and smoothed to give the figures presented. This is the only weekly record of sums of radiant energy. However, Column 6 shows the mean sum of ultraviolet intensities (Coblentz 1945) at Washington 1941 through 1944 for April, May, June, and for September-August, and July. The E-viton is 0.6 of milliwatt minute per cm² and is weighted for maximum erythemal effects at 2,967 mμ. Since the localities, years, and wave lengths measured are different, no comparison can be made except to note the seasonal increase and decrease.

Except for a few localities full sun exposure can be had on the roof of the three or four story building. Measurements of light and other meteorological conditions require space for instruments; this is essential. Technical developments in the past 25 years makes the

measurement of radiant energy comparatively easy (Shelford 1929, Ch. XIV). Furthermore, the control of light by the use of darkness is quite prevalent in physiological studies and exclusive use of artificial lights is not acceptable in ecological investigations.

In order to have plants and animals under conditions of maximum sun exposure, the roof of the building should have a small garden space, a small air-conditioned glass-roofed house for use with animals (and plants under limited conditions). Due to the well-known high toxicity of a minute quantity of illuminating gas constituents, this should be on the main south wing near its south edge so that it is at least 100 ft. from any ventilators, which means that it should be planned from the beginning in the structure of the building. All ducts must be diverted away from spaces for biological use; entrance should be from the roof only. There should be no stairwell from the lower floors in this section of the roof.

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ECOLOGY AND THE SOCIAL SCIENCES

Distinction between ecology and the social sciences is not new (see Novikoff 1945) ; neither is a merging of their disciplines. But, as we appear to be entering a phase of merging (as shown in the number of recent publications on "human ecology," see Deevey 1951), a warning should be posted to remind us of the distinction.

This distinction is simple and basic. We have two groups of relations between organisms and environments. In both of these, any one relation exists only by virtue of an evolutionary past. The difference lies in the mechanism of this evolution.

Ecological relations are in a class with anatomy and physiology; they depend upon the physical inheritance of specific gene patterns. Genes influencing or causing particular relations are selected for or against by the same forces (natural selection) that affect all genes. Evolution in new directions must await the random and uncertain appearance of suitable mutations.

Sociological relations are in a class by themselves; they depend as a group upon the inheritance of a generalized gene pattern, but any one relation is inherited through culture. The latter is learned, can be modified, and need not be handed to the offspring. Selective forces include, for example, belief and persuasion, and evolution in new directions must await the appearance of appropriate ideas.

This distinction is not trivial. It precludes any consideration of homologies between the fields. Only analogies are possible, and it should be remembered that analogies do not increase information.

The two systems of forces, both shaping environmental relations, have produced many interesting analogies. A further alliance through a merging of labels can produce serious and widespread misuse of terms and concepts. Typical examples are the words "society" and "ecology," each well established in both fields. The ecologist uses "society" to describe behaviour patterns that are determined genetically; the sociologist uses "ecology" to describe spatial adjustments that are completely cultural. Even though the users of these terms may not be confused, some of the readers are sure to be misinformed.

Because culture is absent in most species, and negligible in all except man, a study of the environmental relations except those of man includes no sociology. And because genetically determined ecology in man is vestigial, a study of the environmental relations of man includes no ecology (except, of course, applied ecology, man's use of the ecology of other species; see Darling 1951). This division both as to species and processes is fortuitous, and decidedly convenient.

Etymologically, there can be no barrier to the inclusion of the social sciences as a branch of ecology. If this is done, however, a word is then needed to identify that branch of ecology based on genetic evolution. The situation is not without humor; the ecologist, long accused of excessive word-making, is suddenly bereft of a name for his own field.

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NOTES ON THE ROLE OF CRAWFISHES IN THE ECOLOGY OF REPTILES, AMPHIBIANS, AND FISHES

Recently Penn (1950) pointed out that crawfishes are important in the diet of many poikilothermous vertebrates. Data from 108 papers were combined by him into tables and graphs indicating the extent to which certain creatures feed on crawfishes. I wish to comment briefly on Penn's article, to cite additional bibliographic references, to present further instances of predation on crawfishes in the eastern United States, and to discuss other ecological roles played by these crustaceans.

Penn states that "it is surprising that . . . two species of snakes subsist largely on crawfishes" (p. 653). From his graph (Fig. 3), it would seem that these two species are *Natrix e. erythrogaster* and *N. septemvittata*. The frequency of crawfishes in the diet of the former is shown to be 100%. But from the accompanying chart (Table 4), it is seen that this conclusion is based on the stomach contents of only one specimen. Obviously, *N. erythrogaster* should have been omitted from the graph, especially since it feeds mainly on fishes, frogs, and salamanders (Blanchard 1925; Conant 1938; Ditmars 1907; Schmidt and Davis 1941).

Penn's graph for *Natrix septemvittata* is more meaningful, as it is based on the examination of 57 specimens. The feeding habits of this species, and the literature pertinent thereto, have been discussed by Wood (1949).

The inclusion of *Anguilla rostrata, Ameiurus lacustris,* and *Semotilus bullaris* in the graphs might also be misleading, for, of each species, only 2 or 3 stomachs were examined.

The feeding habits of reptiles often vary geographically and ontogenetically. For example, Penn indicates that the frequency of occurrence of crawfishes in alligator stomachs is 87%. This figure is based on 305 specimens from the Sabine National Wildlife Refuge in Louisiana. However, crawfishes were entirely lacking from the stomachs of 74 alligators collected at the St. Mark's Wildlife Refuge in Florida (unpublished MS. of E. R. Allen 1948). McIlhenny (1934, 1935) did not find crustaceans to be important in the diet of the alligator at Avery Island, Louisiana.

Penn soundly concludes that crawfishes are extensively preyed upon by many vertebrates and that more intensive study is warranted in order to utilize the crustaceans to fullest advantage in wildlife management. Further evidence of predation on crawfishes may be gleaned from the following papers (arranged by predator species reported therein):

Micropterus salmoides floridanus (Hubbs and Allen 1943; McLane 1948).

Necturus m. maculosus (Bishop 1926).

Cryptobranchus alleganiensis (Swanson 1948).

Amphiuma m. means (Brimley 1920, 1939).

Amphiuma m. tridactylum (Baker 1937; Chaney 1951; Parker 1937).

Rana clamitans (Babbitt 1937).

Natrix r. rhombifera (Minton 1944).

Pseudemys scripta troostii (Cahn 1937).

I have brought up to date the taxonomy of some of the papers listed above.

From personal experience I can add a few reptiles to the list of predators on crawfishes in the eastern United States. Thus, in the Oconalufty River at the Cherokee Indian Reservation, North Carolina, it was noted that recently captured water snakes, *Natrix s. sipedon,* often disgorged crawfishes. In Rae's Creek near Augusta, Richmond County, Georgia, another water snake, *N. s. pleuralis,* was found to prey frequently on these crustaceans. In northern Emanuel County, Georgia, a water snake, *N. rigida,* apparently subsisted entirely on small crawfishes, judging from 11 food-containing stomachs examined.

Crawfishes were found in the stomachs of 5 soft-shelled turtles, *Amyda ferox agassizii*, from the Savannah River at Augusta, Richmond County, Georgia.

Many species of crawfishes dig burrows from the surface to the water table. The following observations suggest that various fishes, amphibians, and reptiles utilize these burrows for escape from drought and possibly for reinvasion of fluctuating ponds at the end of a dry season.

For several years I collected extensively in northern Emanuel County, Georgia, a region of extensive slash-pine and wire-grass flatwoods. The area is dotted with hundreds of shallow ponds, some overgrown entirely with dwarf cypress (*Taxodium ascendens*), and others with a mixture of dwarf cypress, Ogeechee lime (*Nyssa ogeche*), buttonbush (*Cephalanthus occidentalis*), and various emergent, marginal, and aquatic plants. The ponds yield many species of vertebrates, including the fishes *Gambusia affinis holbrookii, Lucania parva, Elassoma zonatum, Aphredoderus sayanus, Mesogonistius chaetodon,* and *Schilbeodes gyrinus;* the salamanders *Amphiuma m. means, Diemyctylus perstriatus, D. viridescens louisianensis,* and *Siren i. intermedia;* larvae of the salamanders *Ambystoma t. tigrinum* and *A. talpoideum;* tadpoles of the frogs *Rana grylio* and *R. catesbeiana;* and the snakes *Natrix rigida* and *Seminatrix pygaea.* Various other species occur, but the foregoing ones are of especial concern, being mostly of limited vagility on land.

Each year, without fail, most of the flatwoods ponds dry up completely and remain dry for at least 3 or 4 months. In every pond bottom, however, there are a number of crawfish burrows leading down to the water table and sometimes opening into a complex network of horizontal passages. Casual excavation of crawfish burrows during a dry spell revealed several of the forms listed above, namely *Lucania, Aphredoderus, Elassoma, Schilbeodes, Amphiuma,* and *Siren.*

With the advent of hard winter rains, each pond is soon teeming with its usual complement of aquatic creatures. A few of these, such as *Siren* and *Amphiuma,* possibly estivated in the subsurface mud, while others, such as *Diemyctylus, Natrix,* and *Seminatrix,* conceivably migrated overland to the ponds; but a number of forms, such as some of the fishes and the larval amphibians, could not travel far on land or live for any length of time in mud. It seems probable that these forms existed in crawfish burrows during the dry season.

In this area, construction crews often dig sand for nearby road embankments, leaving behind shallow holes which become filled with water during the next rainy period. On one occasion I found a number of adult *Lucania* and an *Esox americanus* in a small, isolated depression which had held water for only 3 days. Several crawfish burrows opened into the pool.

The mosquito-fish, *Gambusia,* often comes to occupy a newly-made pond within a very short time. I hesitate to draw any inference from that fact, however, since these fish are frequently stocked in woodland pools by mosquito control agencies.

The burrows of various crawfishes were described by Hobbs (1942), who also reported finding *Amphiuma means* and *Siren intermedia* in tunnels probably dug by a crawfish, *Procambarus alleni.*

On the northwestern outskirts of Augusta, Richmond County, Georgia, is a creek bottomland supporting a population of salamanders intermediate between *Pseudotriton m. montanus* and *P. m. flavissimus.* From mid-November through February, this bottomland is usually flooded, and the salamanders may then be found anywhere within an area of 10 acres. During the hot and relatively dry summer months, however, they are restricted to a boggy, sphagnaceous strip approximately 120 feet long and 24 feet wide, strewn with rotting logs and debris. In August or September even this strip often becomes dry; but beneath almost every log is a crawfish burrow leading to the water table. In these burrows the *Pseudotriton* are to be found. Usually, each salamander lies in the mouth of a burrow or clings to the muddy wall, and slips into the subsurface water upon being disturbed.

Elsewhere (*in* Goin 1950) I mentioned that the salamander, *Ambystoma c. cingulatum,* inhabits crawfish burrows. This comment merits amplification. *A. c. cingulatum* lives a subterraneous existence, except during a short breeding season in winter. With the advent of near-freezing temperatures, usually in mid-November, these salamanders emerge from their underground retreats. The point of emergence is invariably a crawfish burrow, which generally opens under a fallen log or a pile of debris. The salamanders remain in or near the burrows until the first heavy rains. Some lie a few inches from the burrow mouth, usually facing away from it. These, when disclosed, turn and run into the hole. Others lie with their forequarters protruding from the entrance; these back out of sight when disturbed. Still others are well within the tunnels, and are to be found only by digging. Sometimes 2 or 3 salamanders are noted in the same burrow.

The above observations on *Ambystoma cingulatum* were made each year from 1947 through 1950, in Emanuel and Screven counties, Georgia.

A frog, *Rana areolata circulosa,* also lives mainly in crawfish holes (Wright and Wright 1949, and references therein). This was first pointed out by Thompson (1915), who also gave a good description (*q.v.*) of crawfish burrows.

A snake, *Natrix septemvittata,* has been found in crawfish holes (McCauley 1945).

Certain crawfishes are an important natural check on the spread of the water-hyacinth, according to Viosca (1949). This introduced plant (*Piaropus crassipes*) is firmly established in various states, especially Florida, where it covered 10% of the inland waters in 1949 (Weeks and Bissland 1949). The presence of water-hyacinth reputedly affects game fishes adversely . However, many reptiles, amphibians, and fishes thrive among the submerged rootlets of the plants; and a few forms, notably the salamander *Pseudobranchus striatus axanthus* and the snakes *Seminatrix p. pygaea* and *Liodytes alleni,* are very seldom encountered outside this habitat (Goin 1943). Some of the vertebrates associated with *Piaropus* prey extensively on crawfishes. The part played by these crustaceans in the water-hyacinth community is evidently a complex one.

Summary

Crawfishes are important in the diet of various reptiles, amphibians, and fishes.

Some vertebrates utilize crawfish burrows for escape from drought and possibly for reinvasion of fluctuating ponds at the end of a dry season.

Two species of amphibians usually are inquilines in crawfish burrows.

Crawfishes reputedly check the spread of the water-hyacinth, a plant of considerable importance in the ecology of certain poikilothermous vertebrates.

Pertinent literature references are given.

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REVIEWS

Ecology and Land-use Relationships of Small Mammals on a Michigan Farm [1]

Researchers in small mammal populations have tended, either from lack of funds or man power, to work either on a single species or a single habitat. This publication reports in detail on an extensive study of the various small mammal populations found in the several habitats in a central Michigan locality. It is based on several years work which included intensive field observation and over 55,000 trap days of live trapping and considerable snap trapping. In all over 2,500 animals were handled.

The study of the cropped land indicated that prairie deer mice, meadow voles and house mice made up the bulk of the small mammal population. The deer mice and house mice showed the usual build-up to a maximum density in the fall, but the meadow voles were found to be very scarce during the summer with reproduction starting in the fall and a maximum density in the spring. This was followed, in the years studied, by a crash decline during the spring break-up. This latter is a very interesting observation when compared with reproductive behavior as exhibited in most habitats. There seemed to be considerable difference in population density from year to year.

The woodland areas were occupied mainly by white-footed mice, fox squirrels, red squirrels, flying squirrels, chipmunks, and short-tailed shrews. The squirrels showed more movement from woodlot to woodlot than is commonly thought to be the case.

The treatment discusses the interrelationship between land-use and the distribution and abundance of the small mammals as well as their general population structure. While not a major part of the study a rather detailed report on the predators on the area was made showing their possible relationship to the small mammal populations.

The book is well written and is illustrated with numerous photographs from the area of study. The coverage is good and the discussion well documented with comparisons from the over 180 references listed in the bibliography. Mr. Linduska and the Michigan Department of Conservation are to be complimented on another high quality study.

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[1] **Linduska, J. P.** 1950. Ecology and land-use relationships of small mammals on a Michigan farm. East Lansing: Department of Conservation of Michigan. VIII + 144, 68 figs.

Tampering with Nature in New Zealand [1]

"The problem now is for Man to adapt his activities to the new complex environment around him, but how can he hope to adapt himself to something he knows nothing about? The need for intensive research on ecological problems is obvious."

In commenting thus in the introduction of his book, Dr. Wodzicki emphasizes an emerging awareness that the benefits from introduction of exotics are not always what they seem to be. New Zealand has long been considered the classic example of exotic introductions gone awry. The spread of the red deer over both islands, in numbers that are damaging to the remaining native forest, is well known. The so-called Australian opossum, *Trichosurus*, including several species, was brought in for a possible fur resource, with the result that this vegetarian marsupial has become a problem. With nostalgia for the homeland, the settlers brought in gorse for hedges. It escaped, and has taken over extensive areas. Blackberry vines have thrived too well. The feral domestic goat has become a pest. According to the State Forest Service the "browsing habits of these animals render them second only to deer as destroyers of forest regeneration." Compensating to some extent for this damage, attempts have been made to utilize the goats to control the prolific blackberry. A long list of exotic plants, insects, birds, and mammals have caused New Zealand great concern and expenditure of money in efforts to bring into some kind of equilibrium the disrupted relations of fauna, flora, and soil.

Perhaps it is appropriate to mention that the United States government has even at this late date launched an ambitious program of intro-

[1] **Wodzicki, K. A.** 1950. Introduced mammals of New Zealand. x + 255 pp., 50 figs. (including maps, graphs, and 14 half tones), 62 tables, 4 appendices, bibliography. Wellington, N. Z.: Dept. of Scientific and Industrial Research. Bulletin No. 98. 12s 6d.

ducing exotic game species into this country, and has personnel touring the world to seek species attractive to American sportsmen. With the New Zealand experience before us, one might wonder if our own authorities can claim knowledge precise enough to anticipate the result when a new element is introduced in the delicately balanced state of wild arid lands, for example, or the result when such official action, however carefully done, stimulates the imagination of other, more irresponsible groups.

This new American program is applied to a land already abundantly supplied with wildlife. Exotic introductions were more logical in New Zealand, where the first settlers found no land mammals except a couple of species of bats. Those of us who attended the Seventh Pacific Science Congress in New Zealand in February 1949, missed the familiar rodents. As one American delegate remarked: "If only we could see a little striped chipmunk."

Wodzicki describes four periods in the occupation of New Zealand, which had effect on the native flora and fauna. The first was the settlement of the country by the Maoris in the fourteenth century. They had little effect, however. "Only two species of mammals—the Polynesian rat and the kuri or Polynesian dog—were perhaps introduced during this period." These later disappeared.

The second period began with Captain Cook's visits, 1774 and 1779, which initiated definite introduction of exotics, including such domestic animals as pigs, goats, and later, horses, cattle, sheep, dogs, cats, rats, and mice. Some of these of course arrived accidentally.

The third period, from about 1840 to 1900, was the most important. This was the time of extensive settlement of the country with a growing need for animal food resources for the people and the consequent introduction of more domestic animals. Later, when the economy became stabilized, thought was given to recreation, with growing interest in wildlife for non-utilitarian reasons, resulting in the introduction of many game and non-game animals. In the meantime there had grown up a firm belief that the New Zealand fauna and flora must inevitably go if the country was to be settled, and that European substitutes should be encouraged. The native forests were being lumbered and otherwise cleared away for agriculture. In this new habitat the English skylark and a number of European birds adaptable to agricultural areas were at home.

Then came the fourth period. From about 1907 onward a new trend of thinking developed. This was the period of preserves and sanctuaries for the native flora and fauna, and the growth of a conservation consciousness.

Dr. Wodzicki lists some 53 mammals and 125 birds liberated in New Zealand, of which 34 mammals and 31 birds became established. Many of these have become pests, on a national or local scale. Exotics were drawn heavily from England, 51.6%, notably red deer, rabbit and hare, weasel, and many others. Two came from continental Europe, chamois and small brown owl; from Polynesia, native dog and maori rat (since disappeared); Australia, opossum and wallaby, black swan, and other birds, 16.1%; Asia, tahr, axis, Sambar and Japanese deer, chukar, myna and other birds, 13.9%; America, wapiti, white-tailed deer, moose, Canada goose, California quail and bobwhite, 11.3%.

Some of these, such as the wallaby, are localized and could be eliminated if desired. However, where we found the wallaby on a hasty field trip in 1949, it appeared that it was localized because of a localized habitat in which it happened to have been released. Should it be transferred to a more extensive habitat of that type the problem could be quite different.

One type of introduction was designed to remedy another, as when certain Mustelidae were brought in to control the rabbits and hares that had become a pest. This did not work, ecologically, for, according to certain opinions held in New Zealand, these weasels found the native birds the most convenient food resource. Had a knowledge of weasel food habits been available, this could have been anticipated. On our expedition in the New Zealand Fiordlands, we found few weasels in that particular area. Neither were there rabbits, nor the normal weasel food, mice, in any appreciable numbers. We did find proof of weasels feeding on birds, in the absence of any other dependable food source. This is an outstanding example of the need for ecological information, for which Dr. Wodzicki pleads.

The author discusses each species in considerable detail, its liberation, spread and present distribution, population, economic importance, food habits, and control. He has prepared numerous useful maps and tables, and several appendices, all of which provide in ready reference form a surprising mass of information. The material throughout the book is remarkably well presented. No doubt, this is the most comprehensive and useful publication to date on the exotic mammals of New Zealand. Furthermore, it evinces a promising ecological policy, long held by the author, and reflecting a similar attitude of his agency, the Department of Scientific and Industrial Research.

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Problems of Cytology and Evolution in the Pteridophyta [1]

The reputation the ferns have acquired as being difficult, if not impossible, cytological material has too long been a barrier for investigation in this field. The title of this book does itself serve as a high recommendation of the contents which are almost wholly original in factual data and techniques. Cytologists will be keenly interested in the nature of this previously little known group of plants. As a taxonomic Pteridologist I was interested in the promise of an understanding of the nature of hybrids and the kinds of species. One is not to be disappointed for in a lucid and personable style, such as is only too rare in technical exposition, the author presents the results of some fifteen years of investigations.

Miss Manton introduces her study with a summary of the general picture of polyploidy and hybridization in the Angiosperms. The cruciferous genera *Biscutella* and *Nasturtium* are discussed in detail. In addition the whole subject is further introduced with a chapter on *Osmunda regalis,* an example of a very complete polyploid series in one species. Thus, properly introduced and with the technical terms defined by example, a survey of the British ferns is begun. All of the species are taken up with discussion and illustrations of the pertinent cytology. The taxonomy is discussed in relation to the cytological information and in most cases the two are in close agreement but in a few instances Miss Manton suggests reasons for changes in the classification; or rather reasons for the adoption of one classification in preference to another. The previous investigations of cytologists are integrated into the author's own observations, too often as she apologizes, by way of correction due to improved techniques. The book is much more, however, than a treatment of the cytology of the British Pteridophyta although these have been treated in their entirety for their value as a complete sample. A number of exotic families and genera have been investigated and in many cases Continental species that are closely related to those of the British Isles. The subjects of hybridization, polyploidy and apogamy are discussed at special length. The role of these processes in the evolution of the ferns is considered in the final chapter. Three appendices summarize techniques of preparation and photography, the chromosome counts recorded in the text and the most important facts presented in the book.

The volume is well made and the quality of the paper allows justice to the numerous photographs. The black and white diagrams copied from the photographs of chromosomes are an excellent device. Characteristic leaves, or parts of them, of most species are illustrated by silhouette prints. This method insures accuracy but in many cases gives a heavy print of unattractive appearance.

Of the forty-seven species of British ferns and fern allies, twenty-five of them are polyploid, eleven are of known or presumed hybrid origin and three are apogamous. The percentage of polyploid species is comparable to that of Angiosperms but the level of polyploidy is generally much higher. Definite data is not available for many of the species with high chromosome numbers because lower numbered types or related species (or a sufficient number of them) are not known. But such examples as *Ophioglossum vulgatum,* $n = ca.\ 255$ and the species of *Equisetum,* $n = ca.\ 108$, undoubtedly represent levels above that of tetraploidy. In some genera such as *Dryopteris* a complete series is available. Here in different species and hybrids $2n = 82$ in the diploid, 123 in the triploid, 164 in the tetraploid and 205 in the pentaploid. On less complete evidence *Adiantum reniforme* of Madeira is considered to be decaploid and *Asplenium aethiopicum* from the same island as octoploid.

A considerable number of hybrids are recognized by Miss Manton, some produced in the laboratory and some known only from the wild state. The latter are of three types: those occurring as individual sterile plants, those representing apogamous species and those representing allotetraploid species. *Dryopteris Filix-mas* and *Woodsia alpina* are examples of the last type. Both are considered to be allotetraploids on the basis of the behavior of the chromosomes in pairing in certain hybrids. Hybridization, therefore, becomes an important factor in evolution when it is accompanied by a doubling of the chromosome number or by the initiation of apogamy. Of even greater interest is the possibility of such hybridization occuring more than once and thus causing a polytopic and in a sense polyphyletic origin of a species. As a matter of fact, Miss Manton cites the hexaploid *Polypodium vulgare,* which she somewhat gratuitously considers a distinct species, as such an example.

The reproduction of apogamous ferns is discussed in detail and the unusual complexities in relation to it. Four types of sporangia may be formed, only one of which normally produces functional spores. Spores from any of the other types, if viable, and there is evidence from *Pteris cretica* and *Dryopteris Borreri* that they may be, could be an important factor in evolution. Apo-

[1] **I. Manton.** Problems of cytology and evolution in the Pteridophyta. Roy. 8vo., pp. i-xi + 1–316, with 279 text figures. Cambridge University Press. New York. 1950. $8.50.

gamy is particularly important in triploid hybrids. Miss Manton suggests that triploids are sufficiently out of balance to promote the changes necessary for the induction of apogamy and of course it is necessary if they are to survive as a race. All except one of the known apogamous species are also known to be triploid although some are represented by other levels of polyploidy as well.

Of particular interest to American fern students are the discussions of the *Dryopteris spinulosa* complex, of *Cystopteris fragilis* and of *Polypodium vulgare*. In all three the numerous and intergrading forms existing in the wild are only too well known. Numerous forms, varieties and hybrids have been proposed by taxonomists. Miss Manton, in each case, is able to correlate certain morphological types with a particular cytology and brings, to the extent that the completeness of her studies will allow, a remarkable order out of the confusion. In *Polypodium vulgare* she distinguishes a diploid, a tetraploid and a hexaploid and hybrid triploid and pentaploid.

It is quite evident that these cytological investigations have been most exacting in time, technique and experience and it is not likely that a person trained in another discipline could successfully undertake such work without becoming wholly committed to it. After reading Miss Manton's book, however, taxonomists will undoubtedly hope that someone will initiate such studies on the North American ferns. This would be of particular value in understanding the basis for certain patterns of speciation or variation and also as a strong implement in tracing the history and geography of the species. Only in exceptional cases would it be expected that the cytology would indicate an important revision of the systematics—the genetics and cytology are themselves too strongly expressed in the phenotype the taxonomist studies to expect such a change. However, even when the facts of external morphology are known it is often desirable or even necessary, as in the case of *Polypodium vulgare* cited above, to have a clue to their interpretation and here Miss Manton's type of work would be especially usable.

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Comparative Animal Physiology [1]

Comparative physiology and ecology are areas of biology where effective exchange of data and ideas is bound to have mutually stimulating results. Consequently the publication of an important book in either field is a matter of particular interest to those who may work primarily in the other. Ecologists, therefore, will welcome publication of this comparative animal physiology and want to discover its assets and limitations.

To note these briefly, on the credit side one may cite the following. Here is a comprehensive up-to-date (mainly through 1949) summary of the field of physiology, emphasizing particularly the invertebrate and other comparative material not effectively covered by most existing physiologies (at least in English). Just the bibliographies of the various chapters total nearly four thousand citations while 78 tables, some of them several pages long, present detailed quantitative data drawn from these sources. Here is a wealth of information available in compact form. This is supplemented with more than three hundred illustrations.

Although the text is uneven, it provides at its best an integrated well written précis of a complex and fascinating field. Mention should be made in this regard of the particularly effective chapters on "Circulation of body fluids" and "Chromatophores and color change."

Unfortunately, there are a number of factors which detract from the value of the book as a whole. Perhaps most noticeable is the lack of a strong conceptual scheme to pull the whole work together. This is in part due to the assignment of individual chapters to the various authors without general treatment of overall aspects of problems such as effectors, sense organs, homeostasis, and the like. However, the editor himself has written more than half of the book so that too much individual compartmentalization cannot account for all of this deficiency. It does probably account for the sometimes marked stylistic differences between the different contributors. Notable, for example, is the difference between Prosser's most liberal use of tables and that of the second largest contributor, Frank A. Brown, who uses no tables at all in his 135 pages.

A second general deficiency of the book is the evidence on all levels from editing to binding that more care and thoroughness in preparation should have been exercised. There are, for example, not infrequent errors of fact and expressions of questionable opinions. The Weberian ossicles of teleosts, in fact derived from rib components,

[1] **Prosser, C. Ladd** [editor]. 1950. Comparative animal physiology. ix + 888 pp., 312 figs. Philadelphia: W. B. Saunders Co.

are homologized with the mammalian middle ear bones which originate in the visceral skeleton. Feeding in medusae is quite incorrectly described. On one page the reader is told that the velocity of all chemical reactions in animals is proportional to the absolute temperature, on another that the primary chemical reaction of vision has a temperature coefficient near one. No mention is made of color vision in invertebrates despite the existence of considerable good data, like those of von Frisch on the honey bee.

The human significance of the perception of color is dismissed with the statement, "For civilized man color vision is largely of aesthetic value" (*sic*). Furthermore, in an extended discussion of the chemical mechanisms of vision the quantal nature of light and its relation to vision as shown by the work of Hecht, van der Velden, Baumgarten and others is not even mentioned. Similarly, important recent contributions to comparative sensory physiology by Autrum, Dethier, Debaissieux are ignored. If the reader feels that the book's passages on arthropod compound eyes and ocelli have a faintly familiar ring, he will find the reason in the corresponding passages of Wigglesworth's well-known "Principles of insect physiology."

For their part the publishers have done a generally slip-shod job. Proof reading was poor, indexing inadequate, illustrations and graphs both in preparation and printing frequently leave much to be desired. Design, layout, and even printing stock hardly compare with the high standards the Saunders Company has set in many of their other publications.

Assessment of the credit and debit entries of Prosser's "Comparative animal physiology" suggests that while the work is a valuable addition to the field it is nevertheless disappointing in certain respects both as a research reference and as an advanced textbook. Yet so great is the need for a zoological, in distinction to a medical, physiology that this book is bound to be a useful tool and a stimulating source of information and ideas for many biochemists, ecologists, zoologists and their students.

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Two Significant Publications on the Birds of Mexico

After many years of increasingly rapid adolescent growth, the ornithology of Mexico has begun to come of age, as may be seen from the character of the two publications to be considered.

One of the most urgent needs of ornithologists concerned with the systematics and the distribution of Mexican birds has been for a check-list for the entire republic. With well over 2,200 named forms occurring in Mexico and new ones being described in a steady stream, the task of compiling a list is not an easy one. However, at last this need has been partially met with the publication of Part I of the "Distributional check-list of the birds of Mexico." [1]

The first volume, of the proposed two volume work, covers the families from the Tinamidae through the Trochilidae. To prepare this list the authors have canvassed all the literature and examined collections readily available to them. They, admittedly, did not attempt to examine the many, scattered, smaller collections or those not yet completely identified. Rather than delay the publication of this valuable list, no attempt was made to revise thoroughly many groups which are in obvious disorder, nor were judgments passed on forms of questionable validity. Footnotes are frequently used to note doubtful forms and to express the opinions of the writers. This is a most useful procedure.

The mode of presentation is as follows. Under the scientific name of each species are given the English, Spanish and sometimes various Indian names, and the range of the species as a whole. Each race is treated in the same manner except that ordinarily only a Spanish name is given, and usually this is merely a literal translation of the Latin. Although the check-list has been aimed at the popular student of birds, as well as the specialist, by the inclusion of vernacular names and asterisks to denote races readily identified in the field, one is inclined to question the wisdom of presenting names for all races, especially when they are simply translations, and in Spanish at that, of the original Latin. For example, *Pterodroma cookii orientalis* is translated as "Petrel de Cook Oriental." While attempting to make the check-list useful to the more casual bird student is laudable, it would seem better not to place so much emphasis on races identifiable only by the expert.

In general, the distribution in Mexico of a species or of a race is amplified beyond the mere listing of the states in which it has been found. Often noted are the types of habitats, altitudes, geographically isolated regions, etc., where a form occurs. Also, mention is made frequently

[1] **Friedmann, Herbert, Ludlow Griscom and Robert T. Moore.** 1950. Distributional check-list of the birds of Mexico. Part I. 202 pp., 2 pls. Berkeley, California: Cooper Ornithological Club, Pacific Coast Avifauna, No. 29. $4.00.

of the number of known specimens, dates of occurrence, present abundance, etc. All these data serve to make the list more useful.

Naturally, the check-list has exposed numerous gaps in our knowledge of Mexican birds. Many of these vacancies will be filled as students are stimulated to publish old observations whose value was not appreciated at the time they were made. Other gaps will be bridged by the increasing number of field workers in Mexico. It is apparent that the check-list will soon become obsolete but, as the authors have stated in their introduction, ". . . the rapidity with which, and the extent to which, this check-list becomes out of date will be a measure of its usefulness in advancing knowledge . . . ." Without doubt, Friedmann, Griscom and Moore have made a very substantial contribution toward a more mature Mexican ornithology.

Stemming from his work on the check-list, Griscom has recently published an interesting and controversial paper on the origin and present distribution of Mexican birds.[2] The distribution of the many endemic species and the myriads of endemic sub-species is often so poorly known that it was necessary to restrict the study to the more general aspects of the problem. This has the advantage of making the paper more useful to the biologist who is not primarily concerned with the systematics of birds.

Griscom recognizes seven major elements in the Mexican avifauna: (1) pelagic sea birds; (2) West Indian element; (3) widely ranging element; (4) South American or neotropical element; (5) preglacial relicts; (6) old northern element; (7) modern holarctic element. Nearly every division has several subdivisions as, for example, the South American element which is divided into four parts based on the four generalized distributional patterns which are found.

After listing the species that fall under each of the various elements, the salient facts which may be derived from each group are listed. A welter of conclusions are then presented which are based on the three approaches by which an avifauna may be analyzed, *i.e.*, the ecological, the zoogeographical, and the historical.

So many conclusions are derived from this study it is impossible to consider them all in a short review, but a few of the more controversial should be noted.

The question of the West Indian element in the Mexican avifauna is one which is of particular interest to the reviewer. Griscom presents a list of sixteen species, all of which are found on the Yucatan Peninsula or its adjacent islands, which he considers to have West Indian affinities. This list should be shortened by bringing the systematics up to date, but this is not in order at this time. However, the fact remains that a number of birds do occur on the Yucatan Peninsula and its islands which are otherwise confined to the West Indies, but is there actually a West Indian element in the same sense as the Old Northern or South American elements?

The interesting paper by Bond on the origin of the avifauna of the West Indies (Wilson Bull., 60: 207–229, 1948) casts considerable light on this. Bond believes, and I think correctly, that the avifauna of the West Indies is, fundamentally, of tropical North American origin (Griscom's Old Northern element). He believes that this element, for the most part, was replaced on the mainland by an influx of more aggressive forms. Therefore, it appears that there is no true West Indian element equal to the rank of Griscom's Old Northern or South American elements, but rather the West Indian forms are a part of the Old Northern fauna.

Griscom's list of elements in the Mexican avifauna can be reduced further by placing the preglacial relicts, the pelagic sea birds and the wide ranging elements within the remaining groups. However, for the sake of analyses, these categories are useful, provided one does not place too much emphasis on pigeon-holing and lose sight of the fundamental objective of the study.

Another statement (p. 378) which is rather startling, but common in many zoogeographical studies, is that "The origin of modern orders of birds somewhere in the Northern Hemisphere in Eocene (chiefly) time is clearly proved by the fossil record." This raises two debatable points. First, while the fossil record is better in the Northern Hemisphere and most orders are recorded from there, it is by no means axiomatic that it was their point of origin. In fact, paleontologists often turn from the fossil record and cite the present distribution of the orders as evidence that they arose in the Northern Hemisphere. For example, Matthew ("Climate and evolution," 1939, p. 124), points to the dominately holarctic habitats of the latest and most highly developed groups and the tropical habitats of the most archaic and highly specialized groups, whose ancestors are often recorded from the holarctic Tertiary, as evidence of a northern origin of most orders. It is an example where the ornithologist bolsters his case with the fossil record, while the paleontologist turns to the modern records to support his. This tail-chasing leads nowhere. Although no one has good evidence indicating a southern origin of modern orders, there is no reason to accept without question a northern derivation simply because one set of data is less inconclusive than another set.

The second point which is debatable is that the modern orders arose chiefly in the Eocene. In her recent review of the fossil evidence of avian evolution, Hildegarde Howard (Ibis, 92, p. 3,

[2] **Griscom, Ludlow.** 1950. Distribution and origin of the birds of Mexico. Bull. Mus. Comp. Zool., 103 (6): 341–382.

1950) says, in discussing the marked evolutionary changes during the Cretaceous, ". . . by Eocene time, . . ., most of the orders known today were clearly distinguishable, and several family divisions were apparent . . . ." Obviously, to be so advanced in the Eocene, these orders must have originated in the Cretaceous.

As a whole, Griscom's paper is a rather good one, as compared with the usual run of zoogeographical studies. It is the first to deal exclusively with the complete avifauna of Mexico and therefore many of the pitfalls are not unexpected. It provides a good foundation for future work and is another indication of the growing maturity of Mexican ornithology.

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Cook, Robert C. 1951. *Human fertility: the modern dilemma.* viii + 380 pp. New York: William Sloane Associates. $4.50.

The author of this work, essentially a book-length tract in favor of birth control by carriers of deleterious genes, is the well-known editor of *The Journal of Heredity.* Written throughout in a shrill journalese, it will hardly appeal to the professional ecologist or sociologist, but then it is clearly not intended to. It is aimed at a popular audience, whose members will presumably be aroused to do something by paragraphs like the following:

"Over the entire globe, sixty-eight thousand more people are added to the population each day—today, tomorrow, and an endless succession of tomorrows. Bloated, emaciated, starving babies—armies of doomed infants: that is the inheritance of more than half of tomorrow's children. Each day's addition to the total makes their fate the more inevitable."

The chapters on genetics, as would be expected, are sound, valuable contributions to popular science, though somewhat hyperthyroid in style. The author is also successful in painting a vivid picture of the evils of overpopulation in many parts of the world. His passionate belief in the harmful consequences of fecundity differences between economic and social strata, however, is less convincingly documented; no one will question the desirability of a wise population program, but it is not clear that the author or any other geneticist is in a position to recognize one when he sees it, much less to put it into effect. The case is reasonably well made for the existence of a "modern dilemma" posed by human fertility, but the real dilemma lies in our lack of knowledge about it—a lack that is glossed over in partisan books like this one.

Among the best features of the book are two lively accounts that have little to do with the subject—one of the Scopes trial, and the other of the Lysenkoist controversy. The bibliography lists more than 200 titles, and there is an introduction by Julian Huxley. *E. S. Deevey.*

Macan, T. T., and E. B. Worthington. 1951. *Life in lakes and rivers.* xvi + 272 pp. London: Collins. 21 s. The first popular treatment of limnology in English, this highly satisfactory book, beautifully illustrated by 45 photographs in color and 68 in black and white, is a worthy member of Collins' "New Naturalist" series, of which it is Number 15. The authors, who are among Britain's most capable students of freshwater biology, have set themselves a difficult chore, and have acquitted themselves well. In its most elementary form limnology is an easy subject for popular treatment, for lakes have a strong esthetic appeal, and most people like to fish. But midges and waterbugs, though less banal animals than trout, are less appealing to the uninitiated, and to write a continuously interesting account of limnology that ranges from the origin and postglacial history of Windermere to the biology of sewage effluents, and that distinguishes between morphometric and edaphic oligotrophy or eutrophy, is not a task to be undertaken lightly. The English genius for expository writing has seldom been put to a more challenging test, and while the book falls short of E. B. Ford's extraordinary performance in Number 1 of this series, it is no less highly commendable for that.

Although the book concentrates on British waters and was obviously not written with the interests of American ecologists in mind, its contents seem exceptionally well chosen from this side of the Atlantic. General ecological principles are stressed throughout, and the illustrations from the British fauna and flora are pleasantly unhackneyed when they are not holarctic. The more abstruse aspects of chemical limnology are treated rather summarily, despite fundamental contributions to this subject by Mortimer at Wray Castle, but in their stead the reviewer found the chapters on rivers and on polluted waters remarkably informative. The life of the paralimnion is given due weight, and the interesting story of the introduction and escape of the nutria, *Myocastor coypu,* is brought together, possibly for the first time in a popular work. The problems of productivity and yield are admirably discussed, as are those of fish-farming and fertilization. Subjects that cannot be adequately discussed in a work of this character are not entirely neglected, for there is a full list of key references to the scientific literature of limnology.

It is somewhat distressing for an American limnologist to realize, from certain mild but telling remarks, how some aspects of his subject strike a Briton; but preoccupation with the management of recreational fisheries to the neglect of more fundamental economic problems is a charge that must be borne by American limnology. Although the subject of artificial introduction is not specifically discussed in this book, one can only hope that it may broaden the scientific horizon of American freshwater fisheries experts, particularly those who may be called upon to advise foreign governmental agencies. There is not much time, for "backward nations" have a childish faith in American technical skill, and the large-mouth black bass is in a position to do almost as much harm to the world's food supply as did the domestic goat. *E. S. Deevey.*

Pearse, A. S. 1950. *The emigrations of animals from the sea.* xii + 210 pp. Dryden, N. Y.: Sherwood Press. $5.00. Admiring readers of Professor Pearse's book "The migrations of animals from sea to land" (Duke University Press, 1936) will find this work to be a somewhat expanded second edition. The title has been changed to correspond to an enlargement of the original theme, for in revising the book the author has included material on the invasion of other non-marine habitats, mainly fresh water, by descendants of marine stocks. While this increases the usefulness of the work it has the unhappy consequence of blurring its focus, so that it is more difficult to find the many nuggets of out-of-the-way information it contains. The bibliography has been expanded, but much of the text remains unaltered.

As the first edition has long been out of print, ecologists will be grateful to Professor Pearse and his publishers for making available this improved version. Gratitude to the publishers must be tempered with annoyance, for the price is high, typographical errors are excessively numerous, and most of the photographs are muddy. Gratitude to the author is unalloyed, for despite certain faults of organization the work preserves a small but impressive fraction of a lifetime's research and reading on the part of a distinguished ecologist. *E. S. Deevey.*

Praeger, Robert Lloyd. 1950. *Natural history of Ireland. A sketch of its flora and fauna.* 350 pp. London: Collins. 25 s. A master naturalist, whose knowledge of the Irish fauna and flora is unrivalled, here presents a succinct account of the island he has studied all his life. "Natural history," to Praeger, means primarily systematic botany and zoology with a strong dash of biogeography; the emphasis throughout is on the classical series of questions: How many species in this group belong on the Irish list? Where else do they occur? How did they get to Ireland? A great deal of work, amateur and professional, spanning several centuries, has made Ireland's biota almost as well known as England's. While much remains to be done toward filling in the details, it is clear that Ireland, as the smaller, ecologically less diversified island, has about sixty per cent of the species occurring in Great Britain. In general, the smaller biota has been selected from the larger, but there are a few Irish endemic forms, several supposedly of specific rank, and a few famous disjuncts, of which this book gives an authentic account.

The first important work on Irish natural history appears to be *De Mirabilibus Sacrae Scriptae,* by the 7th century monk, Augustin. It is startling to discover that this early predecessor of Darwin and Wallace discussed island faunas, and maintained that the native animals of Ireland occur there as a result of the severance of a promontory by marine action.

The book is not a systematic catalogue, although the complete Irish list is tabulated for a few small groups of exceptional interest, such as the Amphibia and reptiles. It is a guide to the rather scattered literature, with comments on the most interesting species. In the last two chapters plants and animals are taken up in systematic order, the treatment including a brief account of the history of the study of each group in Ireland as well as an annotated list of references. Flowering plants, mammals, and birds naturally receive the most emphasis, but no group is entirely neglected. A long introductory chapter touches on a variety of matters, from geologic history to regional and ecological geography.

Such a book, falling as it does between two schools of natural history writing, the amateur and the professional, is almost unique. It has the enthusiasm and pride of place of the amateur, but it is thoroughly professional in its scope and in its maturity of thought. It is a pity that the publishers could not spare for it some of the handsome treatment accorded their "New Naturalist Series," for this is a bare volume with only three line cuts and no photographs. *E. S. Deevey.*

ANNOUNCEMENTS

OIKOS

ACTA ECOLOGICA SCANDINAVICA

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Redigenda curavit:

H. O. BACKLUND

Published by: Ejnar Munksgaard
International Publisher and Bookseller
6, Nörregade . Copenhagen . Denmark

Oikos is the name of a Scandinavian periodical devoted to ecology. It is to be the forum of Scandinavian ecologists, although in special cases scientists in other countries are to be invited to contribute.

The main purpose of this new periodical is to collect all important Scandinavian reports on ecologic questions hitherto found in various—often rather inaccessible—special publications. It should, therefore, stimulate contact and cooperation between scientists working in the various fields of ecology—marine, limnetic and terrestrial, zoological as well as botanical.

The periodical will preferably contain original contributions of moderate length, up to 32 pages. The editors particularly wish to emphasize that contributions should deal with causal factors and raise special problems rather than be purely descriptive; this for the benefit of readers not specially familiar with our flora and fauna. One significant part of the periodical will be devoted to critical reports, introducing Scandinavian ecology to scientists in other countries. Naturally, it will be possible to review only works of major importance; articles printed in generally accessible publications on ecology will not be included.

Oikos will appear in half-yearly parts. Annual volumes will contain about 320 pages. It is richly illustrated, the quality of paper allowing illustrations in the text—but particularly detailed photographs will be reproduced on art paper.

The first part contains, besides reports, original contributions from Denmark, Finland, and Sweden.

Of articles on botany, special mention should be made of *Perttula's* studies on the ecology of a number of Eastern Scandinavian plants, their phenology and biology of propagation being compared with their appearance in different habitats; of *Iversen's* investigations into the connexion between the air contents of the roots of various plant species and their occurrence in soils of varying moisture content; and of *Rennerfeldt's* study in the antibiotic effect of various field fungi on a tree fungus.

Zoo-ecology is represented by *Herrström's* article on light preference in a scarabee and the adaptive change in this preference; also by *Hammer's* report on the collection of red clover honey by bees. *Renkonen* describes a method of quantitative investigation of field nematoda that makes it possible to distinguish between nematoda in action and at rest.

Thomasson's contribution is of a limnologic nature: several species of brackish-water plankton have been found among pure sea water plankton in Lake Mälaren, Sweden.

A survey by *Segerstrale* treats of the problem of the Baltic against the background of brackish-water problems in general. *Berzins* describes temperature-conditioned fish migrations in the Bay of Riga.

Vaartaja's investigations into the errors of thermoelement measurements in surface soil and his application of new methods are of great importance to all research in terrestrial ecology.

Various methods of sociological analysis are reviewed by *Renkonen.*

Palmgren demonstrates how periodicity in the mass appearance of mammals and birds may, partially at least, be explained on a purely statistical basis.

The section of reviews and reports deals with most aspects of ecology.

Annual subscription: Danish kroner 40.—, or $6.40 c, or 45 sh 8 d. Obtainable from Einar Munksgaard, International Bookseller & Publisher.

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